

Tandem grip mechanics and tandem linkage shifting in Odonata – reconstruction of evolution and phylogenetic significance

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Received 04 February 2002; revised and accepted 25 June 2002.

Key words: Odonata, dragonfly, functional morphology, caudal appendages, evolution, phylogenetic systematics, flight, Ephemeroptera.

Abstract

The functional morphology of the male caudal clasping apparatus of Zygoptera is compared to that of *Epiophlebia superstes* (Anisozygoptera) and Anisoptera. Hypotheses concerning the mechanics and muscle functions have been advanced by parallel construction of mechanical working models. The evolution of the clasping apparatus and the tandem linkage shifting – from the female pronotum to the head – in the stem group of the Anisozygoptera + Anisoptera (Neoconjuncta) is reconstructed, beginning with a system, which in essential characters resembles that of *Epallage fatime* (Euphaeidae). New acquisitions of the Neoconjuncta, Anisozygoptera and Anisoptera are described and interpreted. An interdependent evolution of the clasping apparatus + tandem linkage and the flight apparatus is discussed. Characters of both systems in the Euphaeidae and the Neoconjuncta are evaluated as synapomorphies, establishing a group Heteronoda. The Zygoptera are substantiated as a paraphyletic group. The functional morphology of the motion system of the cercal and epiproctal filaments of the Ephemeroptera has been studied for comparison. It shows strongly autapomorphous features, adapted to the display flight.

Introduction

Hennig (1969: 323) discussed two central questions concerning Odonata: the problem of interpretation of the male caudal clasping apparatus interrelated with that of mono- or paraphyly of Zygoptera. According to different assumptions concerning homologization of parts and phylogenetic arrangement of groups he mentioned different possibilities:

- (1) Chopard (1949) regarded the unpaired inferior appendage of Anisozygoptera + Anisoptera as homologous to the epiproct (paracercus); the superior appendages were interpreted as cercoids, the “true cerci” were thought to be reduced. In Zygoptera, by contrast, the inferior appendages were thought to represent the true cerci. Hennig concludes that the clasping apparatus of the Zygoptera and the

Anisozygoptera + Anisoptera then could have derived both from a plesiomorphous state, which was composed of cerci and epiproct, since cerci and epiproct are structures of the groundplan of the Pterygota. Alternative apomorphies would substantiate the groups Zygoptera and Anisozygoptera + Anisoptera as monophyletic.

- (2) If however Fraser's (1954) opinion should be correct, that Zygoptera constitute a paraphyletic group, this would prove that the zygoteroid clasping apparatus essentially corresponds to the groundplan of the Odonata and that it was secondarily modified only in the Anisozygoptera + Anisoptera. One could argue that either
 - (2a) the unpaired inferior appendage of Anisozygoptera + Anisoptera is not homologous to the epiproct, but to the cerci, which are secondarily fused – or
 - (2b) that a small 'zygoteran' epiproct has been secondarily enlarged in the Anisozygoptera + Anisoptera and that the "true cerci" have been reduced.

Hennig did not decide between these different possibilities, but he was sure that these questions would be resolved.

It is surprising that Hennig did not consider the essential fact that the male claspers of the Zygoptera and Anisozygoptera + Anisoptera grip the female at different places, namely at the prothorax and head, respectively. Besides this all three alternatives imply difficulties: Chopard's homologization of the "true cerci" and cercoids e.g. is clearly not substantiated (cf. Snodgrass 1954: 33f.; furthermore Chopard's text is partly ambiguous and in his fig. 28A indication lines unfortunately end wrongly). Therefore the possibility 1, in this form, cannot be maintained. The possibility 2a is most unlikely at first sight. Its alternative 2b – the transition of the epiproct from a zygoteroid state to an anisozygoteroid-anisopteroid state – seems also to be difficult to imagine, since the epiproct would be very small initially (but should nevertheless function from the beginning), and furthermore is situated in the zygoteroid state far away from the female head.

Although Hennig's reflections on possible alternatives disregarded essential points of view and partly relied on incorrect homologies, he touched on a circle of problems, the clarification of which could be essential for insights into the evolution of Odonata. Until today, however, these problems have not been studied in detail. There is, e.g., no comparative functional morphological investigation of the male clasping apparatus of odonates, an essential (if not decisive) prerequisite to evaluate whether transformations of clasping structures and (eventually) male-to-female grips could be possible in principle, and one that could also bear on the problem of mono- or paraphyly of Zygoptera.

In the following investigation the nomenclature of Snodgrass (1935, 1954) and Asahina (1954) for the skeletal structures will be used. The names 'inferior appendage(s)' and 'superior appendages', however, are avoided. These are responsible for having misled several investigators, as well as text book authors and popular writers (see e.g. above). For muscles – and of course for joints which have been neglected up to now – my own terminology has been used.

The respective structures of Ephemeroptera, most likely the sistergroup of Odonata, are described first, since the possible pre-existence of structures (e.g. the paraproctal prongs) is of interest. Besides that I hoped to find within this group indications for a reconstruction of an ancient system of terminal abdominal appendages and an ancient moving mechanism. After that a rough description of the different male clasping appa-

tus of the main groups of the Odonata, their morphological constitution as well as basic functions will be given. On this basis I then try to reconstruct in what direction and in which way the different terminal male clasping apparatus and tandem grips have been transformed during evolution. Finally, the consequences for phylogenetic systematics and the possible interrelations to other systems (secondary male copulatory apparatus, flight apparatus) during evolution will be evaluated and discussed.

Material and methods

For the investigation of the skeleto-muscular apparatus animals fixed in Bouins solution or alcohol were used. For first rough estimations — concerning the construction, the mobility of the skeleton and the function of muscles — preparations macerated in KOH were useful. These findings were extended by manipulations of parts from freshly killed animals, if available. Such preparations maintain their flexibility for several months when stored in a refrigerator in a moist atmosphere. The assumptions deduced from these experiments were tested using mechanical working models. For this purpose a special set of custom-made ball joints and hinge joints, which can be combined with Märklin metal parts, was used (Pfau & Koch 1994). The understanding of anatomy, function, adaptive value and paths of evolution also progressed on account of the comparative work itself (i.e. through “reciprocal clarification” = “wechselseitige Erhellung”, Hennig 1950, 1966).

Abbreviations

Definitions and general abbreviations

*[group] — monophyletic group, enclosing all descendants of the last common stem species of all extant species (cf. Hennig 1969: 34)
EMR — epiproctal movement reversal

Skeleton

C — cercus
E — epiproct
La — lamina accessoria
Lam sub — lamina subanalis
Lam supr — lamina supraanalis
P — paraproct
Ppr — paraproctal prong
T — tergum

Joints and axes

j c-p — joint between cercus and paraproct

- $j\ c_1-t_1$ — joint 1 between cercus and tergum
 $j\ c_2-t_2$ — joint 2 between cercus and tergum
 $j\ e-c$ — joint between epiproct and cercus
 $j\ e-la$ — joint between epiproct and lamina accessoria
 $j\ la-c$ — joint between lamina accessoria and cercus
 $j\ la-t$ — joint between lamina accessoria and tergum
 $j\ p_1-t_1$ — joint 1 between paraproct and tergum
 $j\ p_2-t_2$ — joint 2 between paraproct and tergum; this joint is situated in the region where tergum and sternum are fused and may therefore be sternal (cf. also *Ephemera*, Fig. 1).
 $(j\ x-y)$ — joints in brackets label rather flexible joint-like connections (between the elements x and y) = joints with membranous play.
 $v-w/x-y$ — hinge joint axis running through the joints $j\ v-w$ and $j\ x-y$

Muscles

- $mC1$ — muscle 1 of the cercus (in Anisoptera epiproctal) = adc (Asahina 1954)
 $mC2$ — muscle 2 of the cercus = abc (Asahina 1954)
 $mLa1$ — muscle 1 of the lamina accessoria = ada (Asahina 1954)
 $mLa2$ — muscle 2 of the lamina accessoria = $epra$ (Asahina 1954)
 $mP1$ — muscle 1 of the paraproct = ala ($adpp?$) (Asahina 1954)
 $mP2$ — muscle 2 of the paraproct = adv_g (Asahina 1954)
 $mP3$ — muscle 3 of the paraproct = $ppra$ (Asahina 1954)

Functional morphology of male caudal appendages

Ephemeroptera

The last abdominal segment of the male of *Ephemera vulgata* Linnaeus (Fig. 1a) shows (at its distal end, dorso-caudally of the anus) a transverse row of five sclerites, forming a bridge between the left and the right caudal corner of the sternum (St), where the lateral articulation points of the bridge are situated. This bridge consists of two lateral elements (paraprocts, P), two cerci (C) which laterally articulate to the paraprocts via hinge joints ($j\ c-p$), and the epiproct (E), lying between the cerci. The epiproct articulates to each cercus also via a hinge joint ($j\ e-c$). The plates of the cerci and the epiproct support long filaments. At the ventro-lateral and ventro-medial corners, respectively, the cercus and the paraproct articulate with the sternum (via joint $j\ c-st$ and $j\ p-st$, respectively). Dorso-medially the cerci articulate, via joint $j\ c-t$, to an outgrowth of the tergum (T), the tergal suspensory spring (tss). This sclerite crosses obliquely the membranous space between the cerci and tergum on each side; anteriorly it is connected broadly (but elastically) to the main part of the tergum. Dorso-caudally the epiproct merges into a sclerotization, which can be homologized with the lamina accessoria (La) of the Odonata. At its caudal edge the lamina accessoria is connected to the tergum via a broader zone of membrane, which permits a considerable fore-backward translocation of the epiproct. The lamina accessoria is sclerotized weakly and therefore deformable.

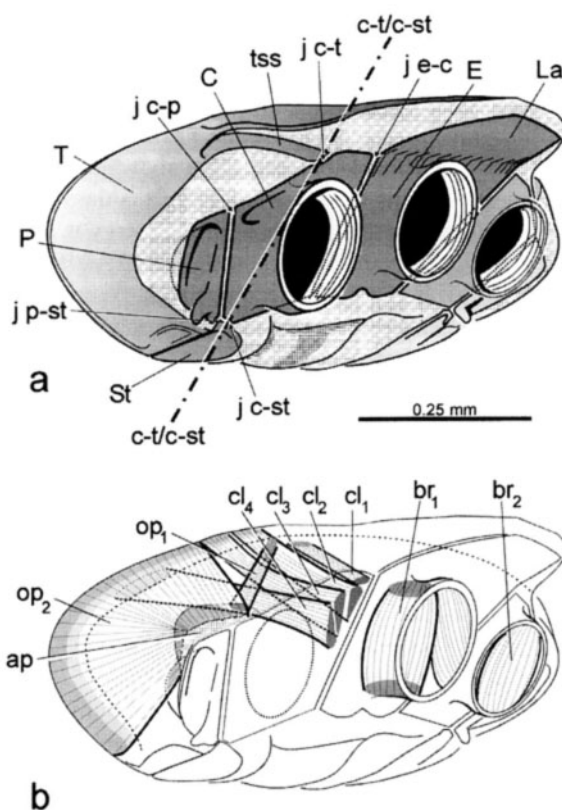


Figure 1. *Ephemerula vulgata* (Ephemeridae), ♂ — last abdominal segment seen obliquely from caudo-lateral; cerci (C) and epiproct (E) cut basally. Schematized with respect to proportions: base of the epiproct e.g. in relation to the cerci is smaller in reality. Lamina accessoria (La) and protruded median part of tergum (T) are lifted. — (a) External view; (b) musculature; cerci, epiproct and tergum depicted transparent; dark grey areas indicate muscle insertions and origins, light grey areas indicate the extension of muscle origins onto the (not visible) tergal antecosta. — ap: apodeme of the opener muscles op_1 and op_2 ; $br_{1,2}$: bracing muscles in the base of the epiproct and cercus, respectively; $cl_{1,4}$: closer muscles of the cercus (+paraproct) and epiproct; j c-st: joint between the cercus and the sternum (St); j p-st: joint between paraproct and St; j c-t: joint between the cercus and the tergum; c-t/c-st: movement axis running through the joints j c-t and j c-st; $op_{1,2}$: opener muscles of cercus (+paraproct) and epiproct; tss: tergal suspensory spring. Further abbreviations see p. 131.

The muscles br_1 and br_2 (Fig. 1b) cross the bases of the epiproct- and the cercus-filaments dorso-ventrally. These muscles are presumably essential for the blood circulation in the filaments, and are considered as of no relevance for the movements of the epiproct and the cerci.

If we consider only those muscles involved in the movement of the epiproct and the cerci two sets of antagonistic muscles can be differentiated: opener muscles (op_1 and op_2) and closer muscles ($cl_{1,4}$). These muscles are arranged (on both sides) laterally and medially, respectively, to a movement axis that runs through the point-joints j c-t and j c-st, which both have ball joint-like characteristics. This oblique hinge joint axis is

designated c-t/c-st according to the joints involved (in Fig. 1 the axis and muscles are illustrated only for the left side). The axis c-t/c-st runs from dorso-medio-frontally to ventro-latero-caudally.

During the opposite movements caused by the opener and closer muscles (Fig. 2) an interesting phenomenon is expected to modify the movements. During the opening (c→a) as well as during the closing (a→c) of the filaments the suspensory spring tss is pressed sideways (Fig. 2b) and by this pressure-spring energy is stored in the proximal connection-region of the tss and the tergum and the tss itself. This situation (Fig. 2b) represents an unstable tilt-over point of the movement. When it is crossed, the tss move back medially and the elastic forces are released and synergistically support the opener and closer muscles, respectively, in the second movement phase (b→a and b→c, respectively).

So at any turning point of the up- and down display flight of *E. vulgata* the opener and closer muscles of the filaments, respectively, on both sides are expected to force the 'bridge' to its instable point, from where it clicks into an opposite, stable position. The divergence and convergence of the filaments thus are accelerated in their respective second phase by the released spring energy of a bistable mechanism. This may be advantageous, since the three filaments quickly snap from stable to stable position, in which they are fixed by the elastic forces of the tss. The filaments are held stable either to slow down the downward soaring of the animal (position Fig. 2a) or to allow a quick ascending flight (position Fig. 2c).

The terminal appendages of *Ephemera* show very particular features, which are quite different from those of the Odonata. To be mentioned here are: the flat last segment, the long cercus- and epiproct-filaments, the sternal articulation of the cerci and the spring mechanism. These can be interpreted as strongly autapomorphous features, adapted to special requirements of the display flight. It is interesting that the paraprocts show a small prong at the ventro-medial side. This might be homologous to the paraproctal prong (Ppr, Figs 3, 4) of the Zygoptera. However, no further indication could be found to support this.

Zygoptera

Morphological details of the 4-part-clasping apparatus of adult male zygopteroid odonates, consisting of the cerci and paraprocts (+ paraproctal prongs), are illustrated for *Calopteryx virgo* (Linnaeus) in Figures 3b-c; the cerci and the paraproctal prongs have been cut proximally in the Figures. The function of this apparatus is complicated, because the cerci possess no precise joints to the tergum. Each cercus is connected on its ventral side to the paraproct via a joint, the j c-p. Furthermore there is dorso-medially a weakly sclerotized connection between the cerci of both sides, the lamina accessoria (La), which is on each side provided with a joint (j la). The joint j la appears to lie inside the lamina accessoria, but the portion lateral to the joint might, alternatively, represent a medio-dorsal projection of the cercus.

Each paraproct is provided with two joints to the tergum, j p₁-t₁ and j p₂-t₂, which define a hinge joint axis p₁-t₁/p₂-t₂ (Fig. 3c) on each side. These hinge joint axes are the only members of the clasping apparatus that are stationary.

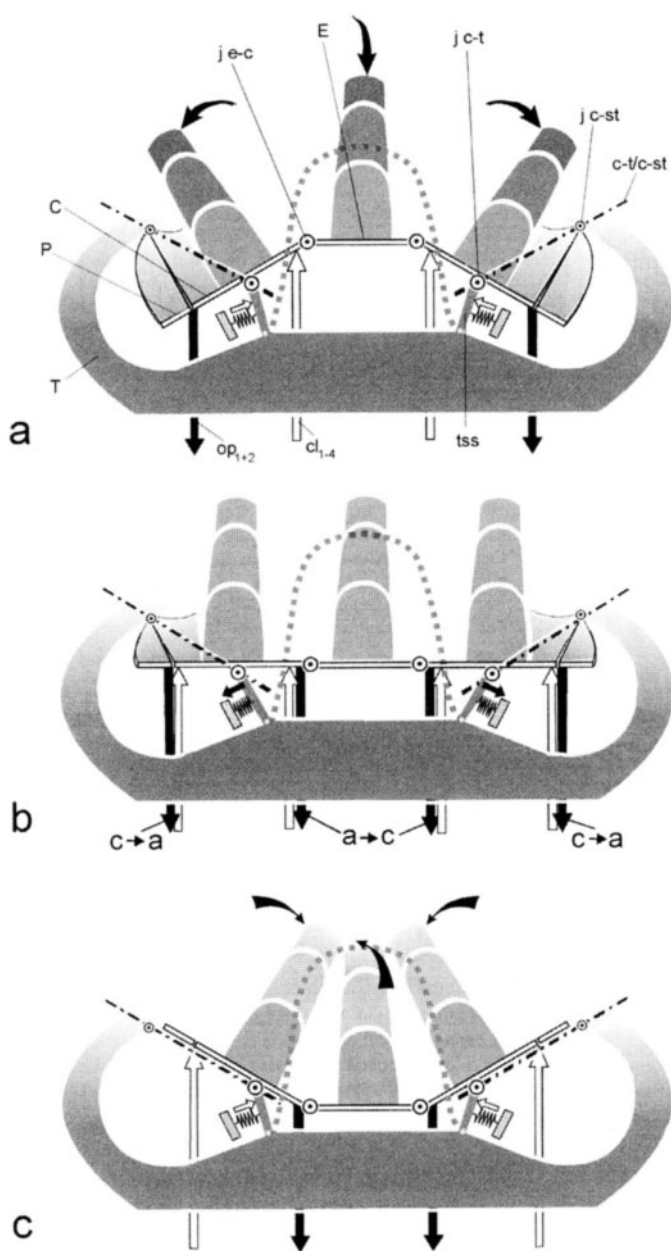


Figure 2. *Ephemera vulgata* — closing ($a \rightarrow c$) and opening movements ($c \rightarrow a$) of cerci+paraprocts and epiproct (diagram). End of last abdominal segment seen from above. The cercus- and epiproct-filaments are shortened. Protruding median part of tergum shown as dashed line. For the superimposed bistable mechanism of the movements, cf. text. — \odot either point-joints with ball joint-like characteristics (j c-t, j c-st) or hinge joints seen in the direction of their axes (j e-c). On account of the obliqueness of the hinge joint axes c-t/c-st there are perspective changes of form, which are only indicated for the lateral part of the cerci+paraprocts. Further abbreviations see Figure 1 and p. 131.

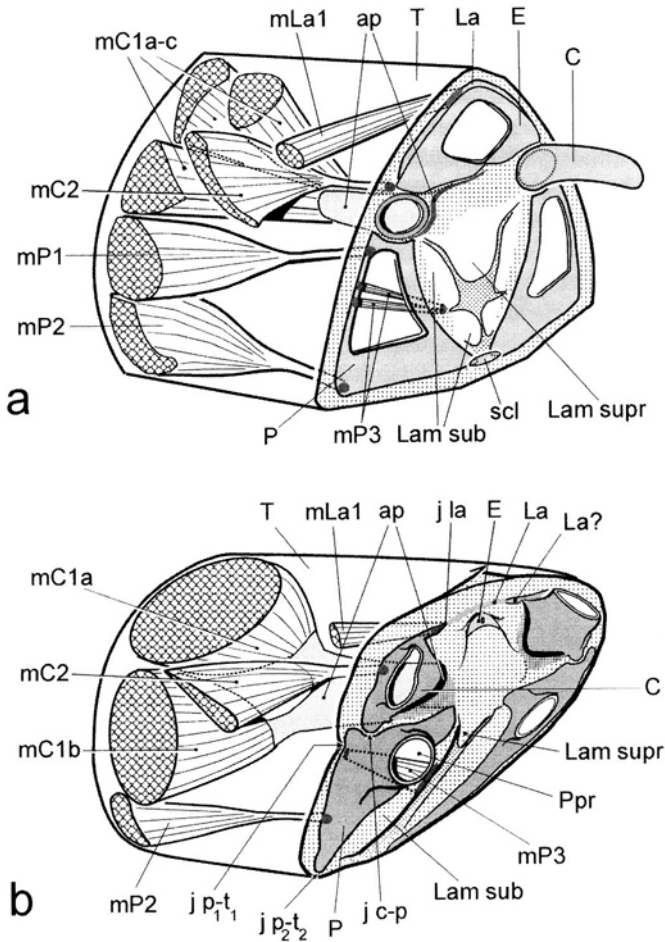


Figure 3a-b. *Calopteryx virgo* — skeleto-muscular system of (a) the last abdominal segment of the larva and of (b) the adult male clasp apparatus; latero-caudal view. Tergum shown transparent. — (a) Only the right cercus is illustrated in full length, left cercus as well as paraprocts and epiproct are cut proximally. (b) Cerci and paraproctal prongs cut proximally. — ap: apodeme of muscle mC1 (the right indication line points to the medial apodeme-invagination, which in (b) forms a deep hollow); this apodeme has been elongated in (b), to show the different connections to the edges of the cercus and paraproct (dotted lines) more clearly. On account of these connections, cercus and paraproct on each side form a close functional unit (see text). scl: ventral sclerite between the paraprocts; further abbreviations see p. 131.

Because of the relative complex musculature – and the poor movement-limitations caused by the flexible dorsal cercus-to-cercus-connection via the lamina accessoria – there are numerous theoretical possibilities of movement. Only those movements which are essential in our context will be considered here.

Contraction of the muscle mP2 opens the paraproct by moving it around the hinge joint axis p_1-t_1/p_2-t_2 . According to the oblique direction of this axis the paraproct moves

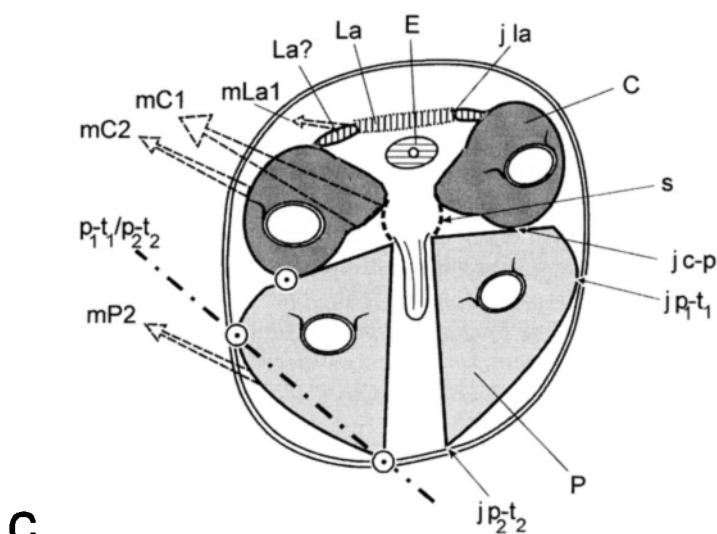


Figure 3c. *Calopteryx virgo* — skeleto-muscular system of the clasper apparatus, shown more diagrammatically. View onto the caudal surface of the last abdominal segment showing the principal arrangement of functional elements of the male clasper apparatus. Cerci and paraprocts (paraproctal prongs) are cut proximally; muscles are only indicated for the left side; apodeme of muscle mC1 (which in reality is dorso-ventrally extended) not shown (cf. Fig. 3b). — ⊙ point-joints with ball joint-like characteristics; j la: joint of the lamina accessoria; s: simplified connection-region between the cercus and paraproct; further abbreviations see p. 131.

ventro-laterally. The cercus is moved together with the paraproct. This is due partly to the existing lever between the joint j c-p and the axis p_1-t_1/p_2-t_2 and partly to the medial connections between the paraproct and the cercus — in Figures 3c, 4, 11 and 15 this connection-region of the mC1-insertion to the cercus and paraproct (which is often rather complex) has been simply indicated by the dotted lines 's'. Since the joint j c-p is moved caudo-laterally during opening, a dorsal movement-component will be added to the cercal movement as soon as the dorsal membrane between the cercus and the tergum is stretched.

The function of a second opener muscle, the mC2, which is connected laterally to the cercus, is different in some aspects. This muscle is able to rotate the cercus alone laterad relative to the paraproct in the joint j c-p. In this case the connection 's' will be compressed and therefore will not pull the paraproct to follow the cercus (as it pulls the cercus to follow the paraproct in the case of the mP2).

The extreme opening of the cerci and the paraprocts of both sides — by strong contraction of the muscles mP2 and mC2 of both sides — moves the lamina accessoria backwards, stretching it laterad and limiting the opening-angle of the cerci+paraprocts.

The strong muscle mC1 (with two portions, mC1a and mC1b) is connected via a broad, dorso-ventrally extended tendon (ap, Fig. 3b) mainly to the cercus, but also to the dorso-medial edge of the paraproct. When the muscle mC1 contracts, the cercal and paraproctal claspers on account of the connection 's' are both moved, i.e. they are closed as a functional unit. There is no individual closing muscle for the paraproct in *C. virgo* as in

certain other species (cf. *Lestes sponsa* [Hansemann], Fig. 11d). According to the oblique movement-axis p_1-t_1/p_2-t_2 the movement of both, the cercus and the paraproctal prong, is oblique, showing a medial and a dorsal movement-component. The cercus however will immediately also perform a movement in the joint $j\ c-p$ – which is directed ventrally, against the paraproct – as soon as the dorsal membrane between the cercus and the tergum is stretched. Altogether the cercus is moved mainly medially – i.e. in a transverse section plane – and the effect of the mC2 (see above) is reversed. During the closing the lamina accessoria is pulled forward and then stretched laterad, thereby limiting the closing movement of the cerci+paraprocts (as during opening, see above).

The clasping apparatus of *Epallage fatime* (Charpentier) is depicted in Figure 4 as a second example for *Zygoptera*, because this system will be of some importance later. Main morphological differences compared to *Calopteryx virgo* pertain to the spatial interrelation of the cerci to the lamina accessoria+epiproct, the dorsal suspension of the lamina accessoria (+epiproct) to the tergum (the lamina accessoria being again only weakly sclerotized), the size and form of the cerci and paraprocts, the force-direction of the muscle mC2 which is strongly oblique and the joint ($j\ p_1-t_1$) which represents a joint with membranous play. In what way these (and further) peculiarities modify the functioning of the parts of the clasping apparatus of *E. fatime* in comparison to *C. virgo* – and are correlated to peculiarities of the male-to-female grip – will be described later.

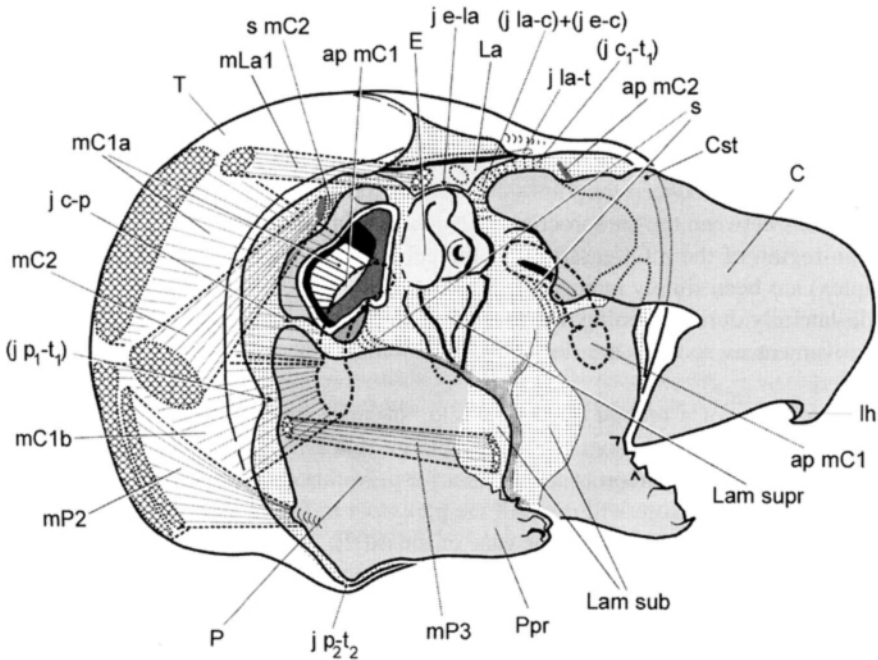


Figure 4. *Epallage fatime* — skeleto-muscular system of the clasping apparatus. Left cercus cut proximally. The mC1b-origin is in reality thicker; it is indicated only partly since it is extended onto the fronto-medial part of the tergum, which is not visible. The apodeme of muscle mC1 (apmC1) is attached to the ventro-medial region of the cercal base; its ventral portion protrudes freely ventrally. The apodeme of muscle mC2 (apmC2) is connected to the cercus via a ligamentous tendon (smC2). — Cst: cercal stop; lh: lateral hook of the cercus; s: ligamentous connection between the cercus and paraproct; further abbreviations see p. 131.

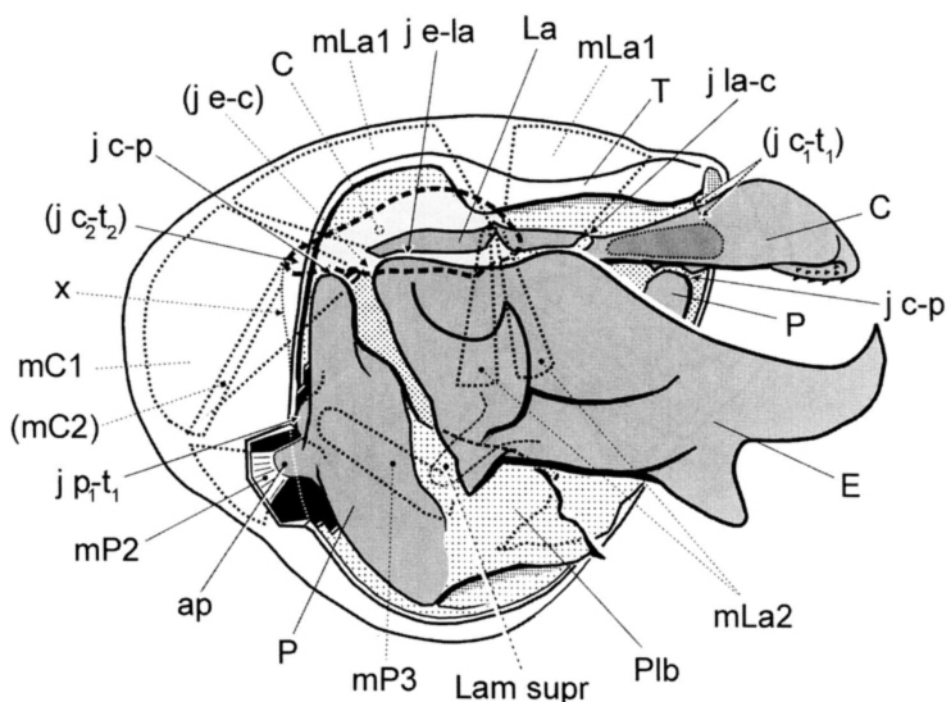


Figure 5. *Epiophlebia superstes* — skeleto-muscular system of the clasping apparatus. Left cercus depicted only as dotted line-contour. For the (hidden) joint-like connection area between the epiproct and the cercus (j e-c), cf. Figure 6. — ap: apodeme of muscle mP2, delivering the lever for the opening movement of the paraproct (and the cerci + epiproct); Plb: paraproctal lobe; x: contour of the membrane between the cercal base + dorsal edge of paraproct and the tergum, indicating the clearance for the forward-backward movement of the system at the height of 'x'. Further abbreviations see p. 131.

Anisozygoptera: Epiophlebia superstes

For a better understanding of the functions of the 3-part-clasping apparatus of *Epiophlebia superstes* (Selys), which consists of the cerci and the epiproct, a mechanical working model consisting only of the essential parts, was built (Fig. 7). Compared to the more realistic morphological aspects depicted in the Figures 5 and 6, it is evident that there is a big step between this greatly abstracted model and the morphological reality. Figure 12a, showing the principal components of the system diagrammatically, may be helpful as an intermediate level of abstraction.

In *E. superstes* the bases of the elements paraproct(right), cercus(right), lamina accessoria+epiproct, cercus(left) and paraproct(left) form a bow (an inverted 'U') which is suspended directly to the surrounding tergum only by two concrete joints, the j p₁-t₁ of both sides. As in zygopteroid odonates the cerci are not connected via distinct joints to the tergum but are dorsally and laterally surrounded by membranous area. However,

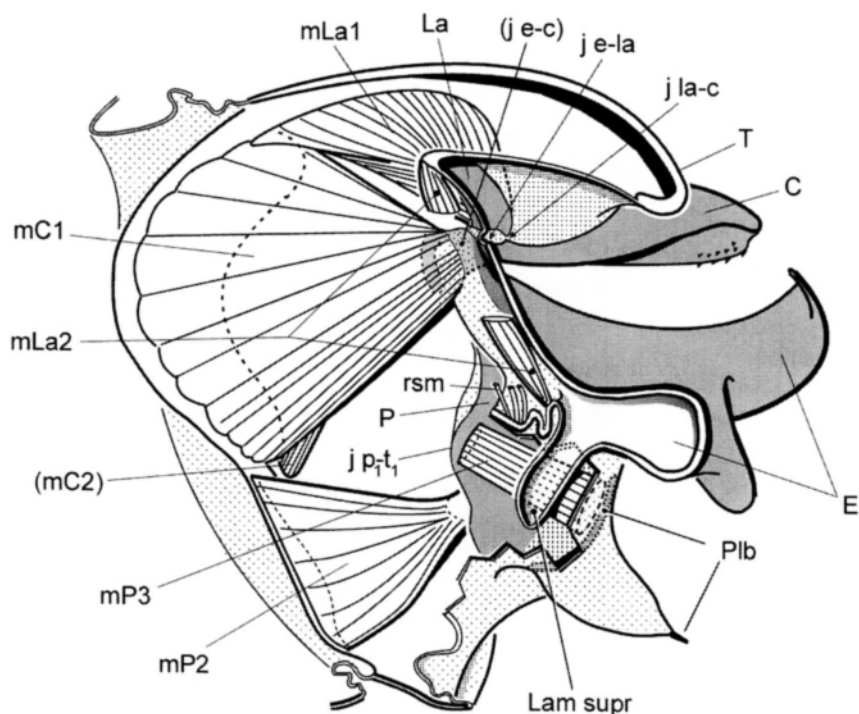


Figure 6. *Epiophlebia superstes* — skeleto-muscular system of the clasp apparatus (mediosagittal section). Rectum cut near the anus. — rsm: rectal suspensory muscles; further abbreviations see Figure 5 and p. 131.

when the cerci are lifted or lowered, two regions in this membrane play a joint-like role and are therefore marked in the figures as joint ($j\ c_1-t_1$) and joint ($j\ c_2-t_2$).

Before gripping and again when releasing the female's head the cerci and the epiproct of *E. superstes* have to be opened (Fig. 8b). Contraction of the muscles mP2 of both sides initiate this action by rotating the paraprocts laterally. Via the dorsal edge of each paraproct and its joint $j\ c-p$ this movement is transmitted to the cercus. The joint $j\ c-p$ is not a pure hinge joint as in the model (Figs 7, 8). It is important however that it does not represent a point-articulation, with ball joint-like characteristics (this would allow a movement of the paraproct around a hinge joint axis $p_1-t_1/c-p$). Therefore the paraproct cannot move much relative to the cercus: the cercus is forced to follow the paraproct-movement, which moves the $j\ c-p$ caudo-laterally. Now the membranous connections of the cerci to the tergum are stretched to their limits at the places ($j\ c_1-t_1$) and ($j\ c_2-t_2$) and the cerci are lifted — each around an oblique axis ($j\ c_1-t_1/j\ c_2-t_2$). On account of the obliqueness of this axis each cercus-tip moves dorso-laterally.

Medially of the cercus, the lamina accessoria and the epiproct are moved caudally via the connection-points $j\ la-c$ and ($j\ e-c$).

The epiproct at its ventral side is attached to the dorsal region of the anus. In the model this suspension was simulated by an elastic ribbon (vs) between the ventral side

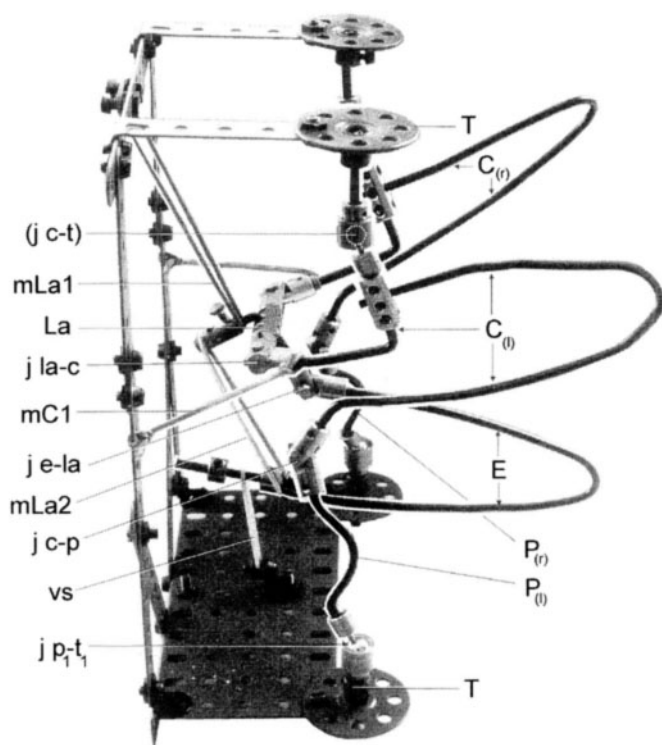


Figure 7. *Epiphlebia superstes* — working model of the clasper apparatus; latero-dorsal view. Simplifications concern (1) the joint-like regions between the cercus and the tergum, ($j\ c_1-t_1$) and ($j\ c_2-t_2$), which were combined in a single ball joint ($j\ c-t$), (2) the lever of the muscle mLa2 on the lamina accessoria, which has been exaggerated in length, (3) the joint $j\ e-la$, which has been shifted ventrally to a larger extent and (4) the joint-like region ($j\ e-c$) which has been omitted. These modifications made it easier to construct the model and to make certain effects clear in a two-dimensional figure. The movements in joint $j\ la-c$ (a joint with ball joint-like characteristics) are attained in the model by attachment of each cercus to the lamina accessoria via a hinge joint, which is also able to rotate around the longitudinal axis of the lamina accessoria. The parts of the paraprocts positioned ventrally of the $j\ p_1-t_1$ (which are unimportant for the function) are omitted. — l: left structures; r: right structures; vs: ventral suspension of the epiproct to the dorsal region of anus (cf. Fig. 6); further abbreviations see Figure 5 and p. 131.

of the epiproct and the base-plate. The angle between the lamina accessoria and epiproct is enlarged in the joint $j\ e-la$ when the lamina accessoria + epiproct is moved caudally during opening (see above) between its dorsal and ventral suspensions: the epiproct is rotated downward in the $j\ e-la$. The muscles mLa2 are also able to enlarge the lamina accessoria-epiproct-angle when they contract. Since the lamina accessoria and epiproct are again 'squeezed' caudally between their dorsal and ventral suspensions (both regions are stretched during this movement), the epiproct and the cerci are both opened. Accordingly the muscles mLa2 are synergists of the mP2, opening the epiproct, cerci and paraprocts from medially, just as the muscles mP2 do this from laterally. In the Anisoptera the function of the muscle mLa2 is in principle the same; since its system has been simplified during the evolution it is less difficult to understand (see next chapter).

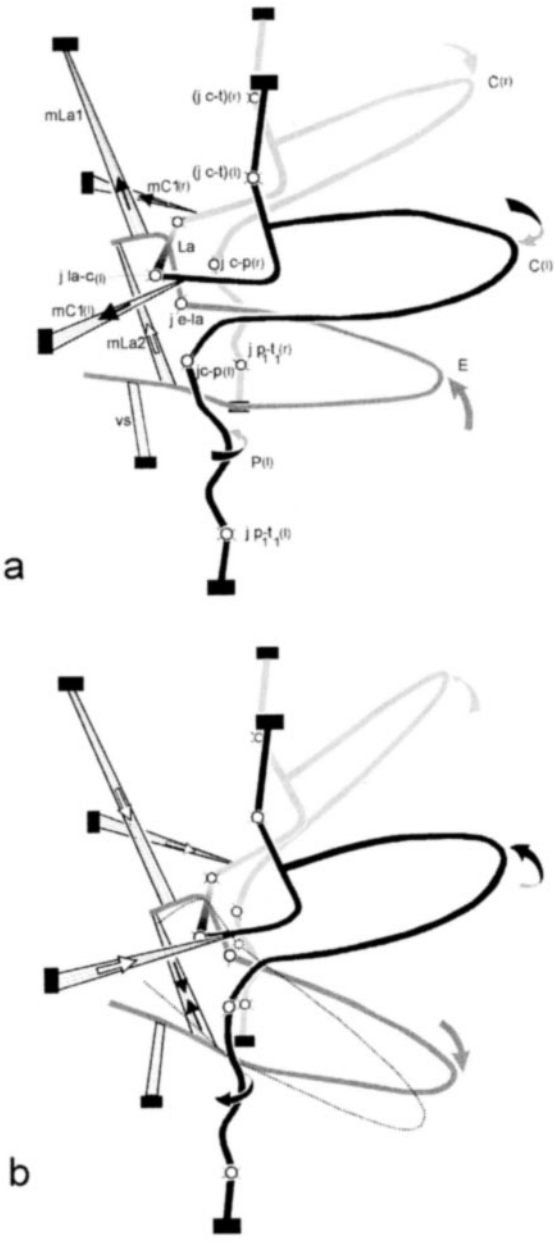


Figure 8. *Epiophlebia superstes* — movements of the working model (Fig. 7), however more simplified. Two extreme positions of the clasping apparatus are drawn from photos of the model: (a) closed system (cerci and epiproct gripping); (b) opened system (before and after gripping). Open arrows inside the muscles indicate stretched muscles, black arrows indicate contracted muscles. Dotted line in (b) shows the passive movement-possibility of the epiproct, which can take place when the system is opened (see text). — □ joints with ball joint-like characteristics; ○ joints with hinge joint-like characteristics; further abbreviations see Figures 5, 7 and p. 131.

The form of the lamina accessoria is rather complicated: it is composed of a left and right part which are both narrowing at their lateral and medial ends. Therefore also the median connection of the two lamina accessoria-halves is joint-like. Left and right halves are bowed forward at this connection-point to form a (relatively small) lever-apodeme for the muscle mLa2.

The joint (j e-c) represents an accessory connection between the lamina accessoria+epiproct and the cercus, which supports the joint j la-c in the mechanical coupling of the structures. Lying on both sides of the hinge joint j e-la it prolongs this joint laterad, without conflicting with the movements of the epiproct in relation to the lamina accessoria and the cerci.

There are two closing muscles of the kinematic system, the mC1 and the mLa1. The model (Figs 7, 8a) shows that the muscle mLa1 is approximately a direct antagonist of the mLa2. The muscles mC1 and mLa1 both move the lamina accessoria+epiproct forward between its dorsal and ventral suspensions, making the angle between the lamina accessoria and the epiproct more acute. The epiproct is moved antero-dorsally towards the cerci, which in turn are moved medio-ventrally towards the epiproct. So the grip of the male on the female is able to exert pressure on both the rear and dorsal sides of her head.

When the opened epiproct is moved passively – i.e. by forces from outside (Fig. 8b, dotted line) – the ventral and dorsal suspension-regions of the system – vs and (j c-t), respectively, in the model – are stretched and produce elastic counter-forces. This elasticity of the epiproct-suspension (which is also present in the Anisoptera) presumably represents an essential detail for a quick ('automatic') grip onto the head of the female. In the first moments of the male's grip the span of the epiproct and cerci may not be enough. The resistance of the female's head may therefore passively enlarge the span of the male epiproct+cerci against the elastic forces; the epiproct can thus be forced to slide over the head, clinging then elastically (i.e. automatically) into the correct place in the moment this is attained. This grip will then at once be secured by the active forces of the male closer muscles.

Even when the cerci are strongly closed via mC1-contraction, the medial elements, lamina accessoria + epiproct, can be actively moved by the male by contraction of the muscles mLa1 and mLa2 to a certain extent relative to the cerci, since the lamina accessoria-halves are movable in the lateral joints j la-c. Besides this the lamina accessoria is able to bend – here the joint-like median connection between the two halves of the lamina accessoria should play a role. On the other hand: on account of this movability and flexibility of the lamina accessoria the lateral system, cercus + paraproct, on each side can correspondingly be moved by the muscles mP2 and mC1 relative to the closed lamina accessoria + epiproct system. It is supposed that these separate movabilities of the median and lateral components of the clasp apparatus are useful when it is necessary to adjust the epiproctal and cercal grips, respectively.

Two further muscles are present:

- (1) The mP3 (Figs 5, 6), a muscle lying inside the paraproct, which therefore has no possibility to affect the kinematic system of the clasp apparatus. It seems that this muscle only opens the anus laterally by pulling the membranous lamina subanalis laterad (the lamina subanalis is not shown in the Figs; for muscle mP3 in Zygoptera, see Fig. 3b).

- (2) The muscle mC2, which could only be found in few specimens, presumably juvenile animals. It represented a rudimentary, thin muscle, extending very obliquely antero-ventro-laterally from the lateral edge of the cercus-base to the tergum. Although this muscle seems not to be functionally important in the case of *E. superstes* it is of some importance as an indicator for the way of evolution: on account of the presence of a similar strongly oblique muscle mC2 in certain Zygoptera (Fig. 4), it is interpreted here as a relic of an oblique opener-muscle of the cercus, which at some time had fulfilled an essential function in pulling the lateral edge of the cercus downwards, opening (= mainly lifting) and rotating by this the cercus (see chapters on evolution).

Anisoptera

The Anisoptera correspond to the Anisozygoptera (*E. superstes*) in the essential aspect that the cerci and epiproct form a 3-part-clasping apparatus, which grips the head of the female. For comparison with zygopteroid and anisozygopteroid clasping apparatus an aeshnid, *Aeshna cyanea* (O.F. Müller), has been chosen.

Here the paraproct has no direct connection to the cercus and therefore participates only weakly in the cercus+epiproct movements. When the opener muscle mP2 of the paraproct contracts (Fig. 9a), the epiproct and cercus are opened via the membranous connection between the paraproct and the epiproct only to a very small degree.

The main muscles to open the epiproct and cerci are the mLa2. The contraction of these muscles squeezes the epiproct postero-ventrally (Fig. 9a). Each cercus is moved by this latero-dorsally, forced by the lamina accessoria movement via the joint j la-c. Besides this it is rotated also around its longitudinal axis, due to the downward-component of the movement of the joint j la-c in relation to the joint (j c₂-t₂). The mode of operation of the muscle mLa2 – which is similar to that of *E. superstes* – is illustrated and explained in Figure 10. This picture also illustrates the principal function of the antagonistic closer muscle mC1, and also that of the muscle mLa1, which is present in most Anisoptera, although not in *Aeshna* and other (all?) Aeshnidae.

The total degree of movability of the cerci is very limited in *A. cyanea*. The opening movement ends when the cerci are stopped by the protruding lateral tergum margins. The closing movement is stopped when a proximal dorsal protuberance of the cercus (Cst, Fig. 9b) meets the dorsal margin of the tergum. Only between these stops the lamina accessoria+epiproct-system is moved together with the cerci; beyond the stops the lamina accessoria and epiproct are moved alone, brought about by a movement relative to the cerci in the joints j la-c and by a certain flexibility of the lamina accessoria.

Compared to *E. superstes* the Anisoptera show essential features, which are in all likelihood apomorphous (for substantiation see chapters on evolution). There are however also interesting plesiomorphous features, e.g. the existence of a small prong on the paraproct, which is interpreted here as a vestige of the paraproctal prong (Ppr, Fig. 9a). Forming the ventral margin of an incision, this prong in *A. cyanea* is part of a security system, which prevents the epiproct to move too far ventrad and laterad in the closed position of the system. In Figure 9b the cerci and the epiproct are moved far beyond the

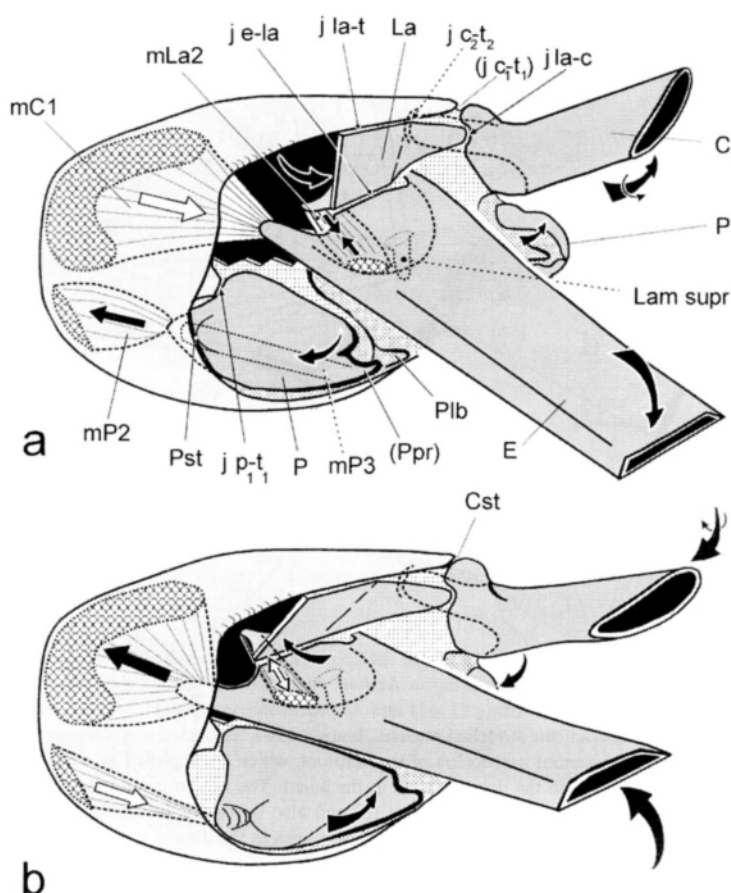


Figure 9. *Aeshna cyanea* — skeleto-muscular system and principal function of the clasper apparatus. Two extreme positions of the clasper apparatus are shown (for mechanics cf. also Fig. 10). Left cercus removed, right cercus and epiproct shortened. (a) epiproct and cercus opened; (b) epiproct and cercus closed to a point beyond the (natural) condition, in which the epiproct and cerci grip the head of the female. Open arrows in the muscles indicate stretched muscles, black arrows indicate contracted muscles. Muscle mP3 (only shown in a) extends from the lateral edge of the paraproct ventro-medio-caudally to an insertion-point on the lamina subanalis (which is not shown), which is situated ventro-medial of the paraproctal prong-vestige (Ppr) and the paraproctal lobe (Plb). — Pst: paraproctal stop, which limits the opening-movement of the paraproct; Cst: cercal stop, limiting the closing-movement of the cercus; further abbreviations see p. 131.

position in which they grip the female's head. In reality the angle between the epiproct and the lamina accessoria is much larger when the head is gripped. Only in this natural gripping-position the lateral borders of the epiproct seem to fit exactly into the distal incisions of the paraprocts. Even then the movability of the paraprocts will allow certain down- and sideward-movements of the epiproct. However, when a paraproct arrives at the adjoining tergal border, the paraproctal stop (Pst, Fig. 9) will prevent a further dislocation of the epiproct.

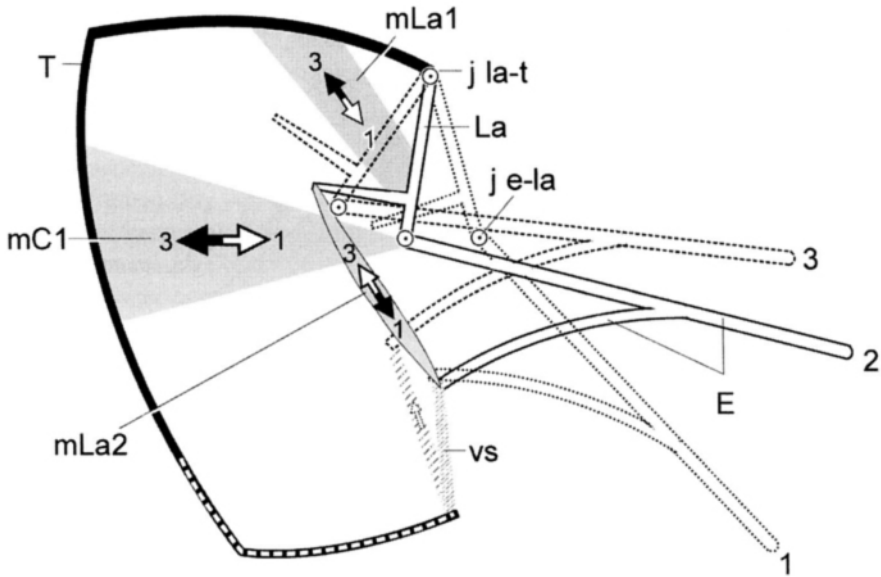


Figure 10. Anisoptera — principal mechanism of the epiproct, more generalized compared to Figure 9 with respect to the muscle mLa1, which is missing in *Aeshna*. Mediosagittal section through the last abdominal segment. Three phases of epiproct-lifting (1→3) and epiproct-lowering (3→1), respectively, are indicated. Open arrows in the muscles indicate stretched muscles, black arrows contracted muscles; numbers indicate the movement-direction. — vs: ventral suspension of the epiproct, which is simplified as a ribbon (in reality the epiproct is connected ventrally to the dorsal region of the anus). The ribbon is stretched dorsally to a larger extent only in the extreme of the lifting-movement (3) and also beyond position (1), when the epiproct is moved extremely downward (not illustrated). ⊙ hinge joints seen in the direction of their axes; abbreviations see p. 131.

For a reconstruction of the groundplan of the *Anisoptera in detail further studies of the clasping apparatus of the sub-groups will be necessary.

Comparison of the principal functions of the different types of clasping apparatus

Zygoptera

Comparing the different types of clasping apparatus in Zygoptera, several constellations of the components could be found (Figs 11a-f). We will consider these types here only in certain aspects, evaluating the principal movability of the bases of the claspers. For a more precise knowledge of the grip efficiency each case should be analyzed with respect to the form of the whole clasping structures (which in many cases is most complicated), with respect to the exact placing and nature of the joints, the dimensions of the lever arms, the points of application and direction of muscle forces and also with respect to the corresponding female structures for tandem linkage.

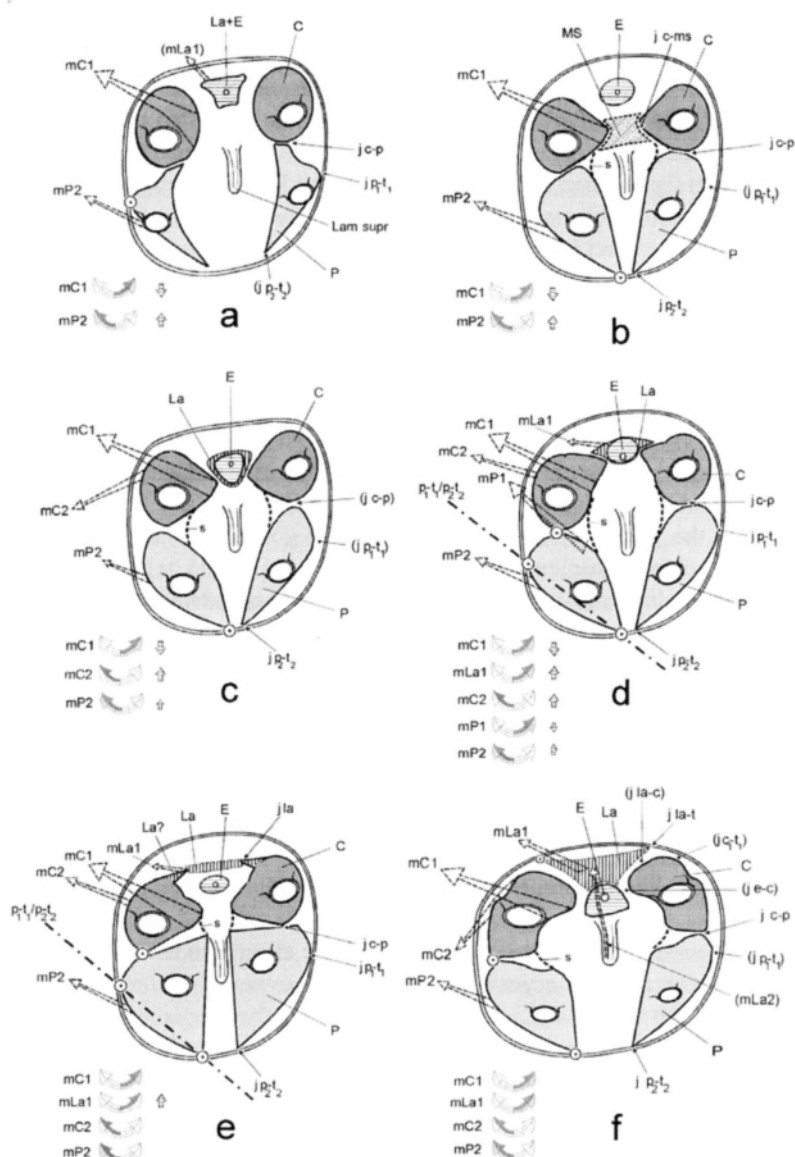


Figure 11. Male clasper apparatus — view onto the caudal surface of the last abdominal segment showing diagrammatically the arrangement of the functional elements in different Zygoptera: (a) *Erythromma najas*, (b) *Coenagrion puella*, (c) *Pyrrhosoma nymphula*, (d) *Lestes sponsa*, (e) *Calopteryx virgo*, (f) *Epallage fatime*. The cerci and paraprocts (paraproctal prongs) are cut proximally. Muscles are only indicated for the left side; the muscle mLa2 is only shown in (f). Apodeme of muscle mC1 (which is dorso-ventrally extended) not shown (cf. Fig. 3b). Muscle functions are indicated for the left cercus and paraproct by bowed arrows (below, left): dark grey halves of arrows concern the cercus, light grey halves the paraproct (muscle mP2 in Fig. 11c e.g. opens as well the cercus as the paraproct). The vertical arrows to the right indicate the muscle effect to the epiproct, i.e. lifting (↑) and lowering (↓) of the epiproct, respectively. — ⊙ point-joints with ball joint-like characteristics; MS: median sclerite; j c-ms: joint between the cercus and MS; j la: joint of the lamina accessoria; further abbreviations see p. 131.

The four elements paraprocts and cerci are arranged in the Zygoptera generally in a bow, a reversed 'U'. Between the cerci different intervening sclerites can couple the left and the right side more or less strongly: In *Coenagrion puella* (Linnaeus) (Fig. 11b) a median sclerite (MS) ventral to the epiproct – apparently formed by fusion of parts of the mC1-apodemes – is involved. In *Pyrrosoma nymphula* (Sulzer) (Fig. 11c) and *Lestes sponsa* (Fig. 11d) the epiproct itself, surrounded by the lamina accessoria, forms a cercus-to-cercus-connection. In *Calopteryx virgo* (Fig. 11e) and *Epallage fatime* (Fig. 11f) the coupling between the cerci is rather weak, since only a weakly sclerotized lamina accessoria (in *C. virgo* split into segments by the joints j 1a) is present. In *Erythromma najas* (Hansemann) (Fig. 11a) the left and right side are largely independent from one another.

These different coupling elements between the cerci of both sides more or less limit the closing as well as the opening movements. The claspers of *C. virgo*, e.g., should be able to open to a relatively larger extent as those of *L. sponsa*. Other limitations are dependent on the more or less loose coupling to the tergum through the joints j p₁-t₁ or j p₂-t₂.

The closing of the claspers is achieved in all cases essentially by contraction of the strong muscles mC1, which mainly move the cerci, but always to a large degree also the paraprocts, via the joint j c-p and/or the tendon-like connection 's'. Only in *L. sponsa* could a specific closer muscle of the paraproct be found (mP1), which – via joint j c-p and the connection 's' – moves also the cercus, supporting the muscle mC1.

In cases when the joint j c-p represents a hinge joint (Figs 11a, b), the cerci and the paraprocts are even more tightly coupled, forming a unit. It is evident that the paraproct must not articulate to the tergum in this case via a hinge joint (composed of joints j p₁-t₁ and j p₂-t₂), since two hinge joint axes in different directions would block the system.

Differences were found in the direction of the forces which are exerted by the closer muscles via the claspers onto the female. In cases where a hinge joint axis p₁-t₁/p₂-t₂ exists (Figs 11d, e), the paraproct is moved according to this fixed axis medio-dorsally during closing (latero-ventrally during opening). Therefore during the closing of the paraproct the contralateral paraproct as well as the contralateral cercus function as opponent structures, as, to a small extent, does the ipsilateral cercus. Oblique hinge joints j c-p between the cercus and the paraproct (Figs 11a, b) are also responsible for oblique directions of the grip forces: in *E. najas* e.g. the forward movement of the joint j c-p, caused by contraction of the muscle mC1, automatically closes the cercus ventro-medially.

The muscle mLal can act as an accessory closer muscle of the cercus+paraproct (Figs 11d, f); in *C. virgo* its closing effect on the cercus, however, is assessed as very weak because (1) the muscle is very weak compared to the mC1 and (2) there is a flexible connection (La?) between the muscle insertion and the cercus.

The opening of the cerci and paraprocts is generated by the muscles mC2 and mP2. The muscle mP2, attached to the paraproct, in every case affects the cercus strongly via the joint j c-p and/or the connection 's', which is stretched. This is true of *P. nymphula* to a smaller degree, because of a rather loose coupling in the joint j c-p; the paraprocts should here be able to open to a certain extent relative to the cerci even when the cerci are held closed. Similar in this respect are species in which the joint j c-p forms a functional ball joint situated far laterally in relation to the paraproct (Fig. 11f). In the cases where the j c-p represents a hinge joint (Figs 11a, b) there is the strongest coupling between the paraproct and the cercus (paraproct-cercus-unit, see above).

Where the joint $j\ c-p$ represents a functional ball joint (Figs 11d-f) the muscle mC2 is able to open each cercus to a certain extent independently of the paraproct; in this case the connection 's' between the cercus and the paraproct is not stretched but compressed during the opening-movement of the cercus. This also applies where a membranous cleft exists between the cercus and the paraproct (Fig. 11c). These possibilities of an opening of the cerci alone (or the paraprocts alone, see above) to a certain extent might be useful in coupled pairs when the grip needs to be corrected while the paraprocts (or cerci, respectively) remain attached and secure this action.

In *E. fatime* the muscle mC2 is strongly oblique. Consequences of its (apomorphic) force direction will be described in later sections.

Cases in which the clasp apparatus is equipped with at least 4 pairs of muscles (mC1, mL1, mC2, mP2), a cercus-to-cercus-connection via the lamina accessoria and a complete set of joints of the paraproct ($j\ p_1-t_1$, $j\ p_2-t_2$, $j\ c-p$) are considered as plesiomorphous (Figs 11d, e). The types illustrated in Figures 11a-c, in contrast, show secondary simplifications of musculature (loss of mC2 or mL1) as well as apomorphic characters of the skeleton, which should be studied comparatively in future investigations with respect to occurrence in different groups and phylogenetic relevance.

The epiproct in the adult Zygoptera represents only a small knob, showing a gland aperture at the tip. Nevertheless it is most interesting (see later chapters) to pay attention to the epiproct-movements during the closing and opening of the cerci and paraprocts. If we imagine for the case of *C. virgo* the epiproct as a longer structure directed caudally, the tip of this median prong would be moved *upwards* when the muscles mL1 of both sides would contract, pulling the joints $j\ la$ and the lamina accessoria forward. The epiproct is moved upwards and sideways (towards the side of the contracted muscle) if only the muscle mL1 of one side contracts. The performance of these movements of the epiproct is probably the main function of the muscle mL1 in *C. virgo* – possibly in the context of the distribution of the secretion of the epiproct-gland. With respect to the closing of the cerci the muscle mL1 in *C. virgo* is to a far extent synergistic with the mC1; its closing effect however is poor in *C. virgo* (see above). If one regards the effect of the muscle mC1 on the epiproct, only a small effect of downward-rotation is present in *C. virgo* (on account of the large membranous area between the cercus and the epiproct), only suggesting an antagonism between the muscles mC1 and mL1.

The antagonistic actions of the muscles mC1 and mL1 with respect to the downward-upward-movements of the epiproct result from the fact that the medial part of the cercus (which functions as a lever) protrudes *ventrad* of the epiproct (i.e., the epiproct is situated dorsally of the cerci; this primitive condition also occurs in females and larvae, Figs 16, 3a). This mC1-mL1-antagonism is more evident in those zygopterans, in which the epiproct and the cerci are less separated or articulate directly to one another (as e.g. in *L. sponsa*). In these cases the epiproct is moved strongly downwards when the muscles mC1 contract to close the cerci and the paraprocts; it is moved upwards when the mL1 contract.

In *E. fatime* experiments instead indicate that the muscles mL1 and mC1 function as synergists with respect to the epiproct. Furthermore the net movement of the epiproct is largely 'neutral': a small dorsal movement of the epiproct in the joint $j\ e-la$ relative to the lamina accessoria and a small ventral movement of the epiproct together with the

lamina accessoria (around a hinge joint axis la-t/la-t) seem to neutralize one another when the muscles mLa1 or mC1 contract. The synergistic functions of the mLa1 and mC1 are mainly due to the spatial interrelation of the cercal lever to the lamina accessoria + epiproct, the evolutionary consequences of which will be examined in later chapters.

Anisozygoptera and Anisoptera

The situation in the Anisozygoptera (*Epiophlebia superstes*) and the Anisoptera is illustrated in Figure 12. Here, instead of the two ventral paraproctal prongs, the unpaired long epiproct works as an opponent structure of the cerci. The cerci of both sides are coupled via the lamina accessoria + epiproct or only via the lamina accessoria, just as in (primitive) Zygoptera. The muscle mC1 shows a clearly different insertion only in the Anisoptera, where it represents a muscle of the epiproct. A certain muscle of the Zygoptera, the mC2, was not found in (adult) Anisoptera, but in *E. superstes* there is sometimes a vestige of it. In *E. superstes* and in the Anisoptera a further muscle is engaged in the opening of the clasp apparatus, the muscle mLa2, which is present, but not engaged in this function, also in the Zygoptera (it is indicated only in Fig. 11f).

The cerci in *E. superstes* (Fig. 12a) are connected via the joints j c-p to the paraprocts and via broader membraneous regions to the tergum, similar to the situation in the Zygoptera. In the Anisoptera (Fig. 12b) the connections of the cerci to the paraprocts have been loosened; instead the cerci have acquired direct articulations to the tergum (joints j c₂-t₂).

Most obvious is that the movements of the epiproct differ in the Anisozygoptera + Anisoptera from those of the Zygoptera (Figs 11, 12: vertical arrows below left). The significance of this difference and the reconstruction of its evolution will play a major role in the following sections.

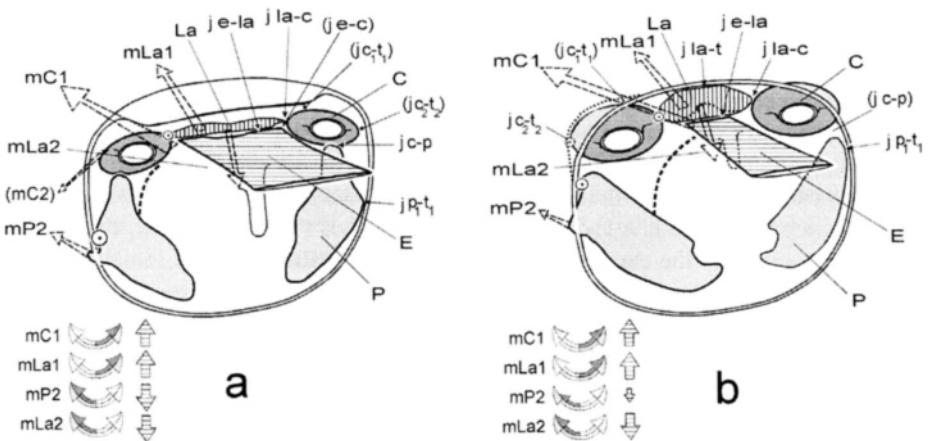


Figure 12. Male clasp apparatus — view onto the caudal surface of the last abdominal segment showing the principal arrangement of the functional elements in (a) Anisozygoptera (*Epiophlebia superstes*) and (b) Anisoptera. Cerci cut proximally, epiproct shortened. Muscle functions are indicated as in Figure 11. — ⊙ point-joints with ball joint-like characteristics; abbreviations see p. 131.

Evolution of the clasping apparatus and tandem linkages

Arguments for the 'epiproctal movement reversal' (EMR) and the direction of evolution

There has been some confusion concerning the terms 'inferior appendage(s)' and 'superior appendages'. Chopard (1949) e.g. wrote, that the inferior appendage does not exist in the females of the Anisoptera (see also Introduction). His homologization of the inferior appendage with the epiproct in the males of Anisoptera is therefore difficult to understand. Possibly this induced Hennig (1969) to infer that the inferior appendage might be homologous to the fused "true cerci" (point 2a in the Introduction; for confusion concerning the nature of the inferior appendage, cf. also Pinhey 1969: 143). This homologization cannot be maintained, since paraprocts and cerci exist besides the epiproct in all groups, the paraprocts in Anisozygoptera + Anisoptera however without the paraproctal prong of the Zygoptera.

When we try to reconstruct the evolution of the clasping apparatus of the odonates, the structures in the common ancestor of *Odonata and their transformation towards the morphology of extant groups both have to be reconstructed. Many authors regard the clasping apparatus of Anisozygoptera + Anisoptera as the apomorphous system, partly on account of the fact that Anisozygoptera and Anisoptera share other characters which are most probably apomorphous (Asahina 1954). However, it is hard to find any profound argument within the literature, which confirms the apomorphous nature of the cerci+epiproct-claspers of the Anisozygoptera + Anisoptera.

Hennig's alternative 1 – concerning the possible monophyly of Zygoptera and Anisozygoptera + Anisoptera on account of an alternative modification of the groundplan of the anal appendages (see Introduction) – is judged here as not correct in its presented form on account of wrong homologies. But a similar conclusion can be made after the wrong homologies (paraproctal prongs = true cerci) have been corrected: the possession of a long epiproct in combination with the cerci in Anisozygoptera + Anisoptera could be interpreted as the most primitive equipment of the Odonata, again with the argument that both structures belong to the groundplan of the Insecta and are also present in the larvae of all groups of Odonata (including the Zygoptera). This would contradict the (tentative) assessment of many authors (which nevertheless is correct, see below).

As briefly mentioned in the Introduction, the different locations where the male claspers grip the female are of great importance. Any reconstruction of an ancient male clasping equipment must consider this difference. Several combinations of gripping structures and grip-places on the female are imaginable, which could theoretically represent the primitive situation of the stem species of *Odonata. However it would be troublesome to go through all these possibilities, to check their likelihood and to exclude the one or the other. It is more realistic to go back to our knowledge concerning the pair forming and the functional morphology as demonstrated by the extant species, and to look for concrete indications. For instance:

- (a) We can take for granted that the Odonata represent a monophyletic group. This means that the common ancestor of all extant species already copulated forming a pairing wheel. We can be very certain that the pairing wheel is a homologous feature of all odonates, since (1) it is most certain that the secondary male copulatory apparatus already existed at the base of the *Odonata (in a largely zygoteroid differentiation;

Pfau 1971), and (2) the males always have to grip the females *at first* with their terminal claspers and afterwards form the pairing wheel by coupling also via the secondary copulatory apparatus. It is therefore unlikely that an evolution of different (alternative) clasping modes might have followed the evolution of the secondary copulatory apparatus. It is more likely instead that one common primary mode of clasping already existed at the base of the *Odonata.

- (b) The possibility of an intermediate grip position – i.e. in between the head and the prothorax, in the neck region of the female – can be regarded as unlikely on account of the fact that this location in the female is thin and weakly sklerotized.
- (c) The possible consideration that the head was the primitive gripping place can be considered as less likely, since there are indications that this linkage is very advantageous. It is unlikely that a favorable linkage should have been abandoned. In addition there are characters in the anisozygopteroid-anisopteroid clasping apparatus which are most likely apomorphic (see later sections).

The epiproct is normally situated dorsally of the cerci in insects. This is also the case in odonate larvae (Fig. 3a), odonate adult females (Fig. 16) and in (most) adult males of the Zygoptera. It is therefore likely that this is the primitive position of the epiproct in the Odonata. On account of this position in the larvae of odonates all terminal appendages (epiproct, cerci and paraprocts) were closed – i.e. moved ventrally and medially, respectively – when the mighty muscles mC1 contract.

In adult males of Anisozygoptera and Anisoptera the epiproct lies between or slightly ventral to the cerci – at least as far as its relation to the main lever-points of the cerci is concerned. This is a derived state. In this position the epiproct will not move ventrally like in the (primitive) Zygoptera (Fig. 11) – or in the females – when the muscles mC1 contract. Instead it rotates *dorsally* (Figs 8a, 9b, 10, 12). This means that the movement of the epiproct is opposite to that of the primitive state in the Anisozygoptera + Anisoptera. The evolution of a gripping function of the epiproct in the Anisozygoptera + Anisoptera therefore requires an epiproctal movement reversal (EMR) at the beginning.

Theoretically a lowering (= ventrad movement) of a primitive epiproct, i.e. of a long structure which is situated dorsally of the cerci, via mC1-contraction could also create a grip, since the epiproct would work ventrally, i.e. also against the cerci, and could be usable as their opponent structure. Such a grip however is not represented in extant Odonata. On the other hand, if such a grip would have existed at the beginning of the Anisozygoptera + Anisoptera, there would have been no chance for the epiproct to reach and grip the head of the female: during the necessary EMR the epiproctal base and the cercal bases would have to change positions in relation to one another and would go through states, in which the involvement of the epiproct would come to a standstill. During this standstill no cercus-lever effect would have been present to cause an opposing movement of the epiproct against the cerci. Furthermore we can principally conclude that it is unlikely that the EMR took place with an epiproct as a long structure: in the middle position of the EMR a long epiproct would not only come temporarily to a functional standstill but would also hold the female apart instead of clasping her. These reasons indicate that the EMR took place in a system, in which the epiproct was a small structure and presumably had a quite different function than gripping.

Based on these arguments, it seems unlikely that the anisozygopteroid-anisopteroid equipment – consisting of three structures, two cerci and one long epiproct situated ventrally of the cercus-leverpoints – is primitive (although this first seemed to be close at hand). Similar considerations argue against the possibility that an equipment consisting of 5 gripping parts – a long dorsal epiproct, two cerci and two paraproctal prongs, i.e. a most complete equipment – was the primitive one and was secondarily transformed in alternative ways to the zygoteroid and the anisozygopteroid-anisopteroid states.

Summarizing this we can assume that a small, dorsally situated epiproct – which was not involved in gripping and which moved in a primitive way, i.e. rotated ventrally when the closer muscles of the cerci contracted – and two cerci – which should have been the primary clasping structures in the stemgroup of the Odonata – should have been present in the primary equipment of the last abdominal segment of the males in the *Odonata. As the primary gripping place of the cerci we stated that the female pronotum is the most likely location; the primary linkage was therefore to a far extent zygoteroid and the linkage-shifting must have gone from the prothorax to the head during the evolution of the Anisozygoptera + Anisoptera and not vice versa.

Now we have to consider the question whether the paraproctal prongs already existed in this early state, assisting the cerci in gripping, or not. Again there exist different possibilities which implicate different phylogenetic conclusions.

- (1) The ancestor of *Odonata may have been equipped only with cerci which anchored to the female pronotum. The further evolution might have gone in different directions: (a) to the Zygoptera, where the paraproctal prongs were formed to assist the cerci and (b) to the Anisozygoptera + Anisoptera, where the epiproct (after an EMR) was prolonged and achieved a role in assisting the cercal grip on the female prothorax; this grip then shifted towards the head of the female. This would mean that the groups Zygoptera and Anisozygoptera + Anisoptera on account of alternative-apomorphous clasping apparatus are both substantiated as monophyletic groups.
- (2) The primary male clasping apparatus may have consisted of cerci and paraproctal prongs, anchoring as a 4-part grip on the female pronotum as in the Zygoptera. This grip was then not fundamentally changed at the base of the Zygoptera, in which apomorphies involving other body systems evolved. At the base of the Anisozygoptera + Anisoptera the EMR, the prolongation of the epiproct and the grip-shifting occurred as in (1). Again Zygoptera and Anisozygoptera + Anisoptera would both represent monophyletic groups. Not considering details (EMR etc.) this is in principle the opinion of Lohmann (1996).
- (3) This possibility corresponds to (2) as far as the primary clasping apparatus is concerned. However, no apomorphous characters have been evolved constituting a monophyletic group Zygoptera. Instead in a certain zygoteroid branch the EMR was initiated. It took place subsequently in a zygoteran lineage that led to the Anisozygoptera + Anisoptera. In this line the epiproct was elongated and the epiproct+cerci shifted from the female pronotum to her head (just as in 1 and 2). This possibility would indicate that Zygoptera are paraphyletic. The Anisozygoptera + Anisoptera again (as in 1 and 2) would form a monophyletic group – of course also on account of further apomorphous acquisitions.

If we look more closely on the extant clasping apparatus and mechanisms, we can support the assumption of an ancient zygoteroid gripping system consisting of cerci and paraproctal prongs and so exclude possibility (1). It is a stroke of luck that *E. superstes* has survived to present. In this genus the head is gripped by the anisopteroid large epiproct. The main closer muscle mC1 of the cerci and the epiproct however is still a cercus-muscle, but already with a slight tendency of its insertion towards the epiproct. This essential aspect was already taken into consideration by Asahina (1954: 76 “Might it be a Zygoteroid feature?”; in this paragraph “ada” has been erroneously printed instead of “adc” = mC1). Although the paraprocts show no prongs in *E. superstes* – only a soft lobe which is considered here to be not homologous to the paraproctal prong (Fig. 16) – they still work closely together with the cercus+epiproct-system, indicating that in the ancestral species, from which the anisozygoteroid-anisopteroid line had evolved, the paraprocts were involved in gripping. Since the cercus-paraproct-connection has been practically eliminated in Anisoptera, indications of this transition would have been lost without *Epiophlebia*. A further support to this argumentation is the small prong of the paraproct in *Aeshna cyanea*, occurring only in males, which has been homologized here as a vestige of the paraproctal prong (Fig. 9a).

According to the above considerations – and the comparative results described for the Zygotera – the clasping apparatus of the ancestor of the *Odonata can be determined to a far extent as lestoid-calopterygoid.

Since no clear synapomorphies constituting a monophyletic group Zygotera could be found hitherto (Pfau 2000), we are not able to substantiate a monophyletic group Zygotera – the second possibility – up to now. So we cannot yet exclude the third possibility. Just as in the case of *Epiophlebia superstes*, where some special characters have been conserved, which support a certain direction of evolution (and, e.g., a pre-existence of the paraproctal prong), the possibility exists, that a zygoteroid species (group) could have been ‘conserved’ until today that already shows the beginning of a transformation of a zygoteroid 4-part-grip (= cercus+paraproct-grip) towards an anisozygoteroid-anisopteroid 3-part-grip (= epiproct+cercus-grip). In other words: it is possible that in an extant zygoteroid odonate a clasping apparatus could be found which fits in between the Zygotera and Anisozygotera + Anisoptera, indicating the beginning of an evolution in the direction of the Anisozygotera + Anisoptera. Considering the paraphyly-hypothesis of Fraser (1957), which has not been rejected up to now by strong arguments, a pre-adaptive construction of a clasping apparatus, from which an evolution towards the anisozygoteroid-anisopteroid apparatus could have started, should be searched at first in the calopterygoid groups of zygoteroid odonates. Indeed a possible model of an ancestral starting point was found in the calopterygoid odonate *Epallage fatime*.

Epallage fatime – extant model of a zygoteroid starting point towards the Anisozygotera + Anisoptera?

In *E. fatime* (Figs 4, 11f) the epiproct represents a small sclerotized protrusion as typical for the Zygotera. However in *E. fatime* the epiproct is situated between the cerci – and it is the dorsal region of the cercus-base, which protrudes mediad towards the epiproct. This dorsal cercus-region protrudes lever-like to the dorsal edge of the epiproct, approxi-

mately to the place where the lamina accessoria is attached (via the joint $j\ e-la$) to the epiproct. The different positional relationship between the cerci and epiproct is presumably due (1) to the (anisopteroid) dorso-ventral compression of the abdominal segments and (2) to an alteration in the function of the cerci, manifested mainly in the extreme dorsal insertions of the muscles mC2 on the cercal bases; from there the mC2 extend strongly oblique ventro-latero-frontally.

Presumably the (apomorphous) attachment and direction of the muscle mC2 is the main reason for the new orientation of the cercus in relation to the epiproct and lamina accessoria. Since the cercus-base has been protruded dorso-medially – as well towards the dorsal tergal region as towards the lamina accessoria+epiproct – a close dorsal suspension and left-to-rightside coupling of the cerci has been attained. Furthermore it is obvious that the muscle mC2 has now a long lever arm with respect to the joint $j\ c-p$ and produces new force components for the cercal movement:

When the muscle mC2 contracts the cercus is moved on account of the direction of its force (1) laterally (the hitherto main component of the movement; e.g. in *Calopteryx virgo*), (2) dorsally (stemming the joint $j\ c-p$ caudally and the paraproctal prong ventrally) and (3) around its longitudinal axis. The large, flat main hook of the cercus, which points antero-ventrally in the (extremely closed) resting position (Fig. 4), is rotated on account of the 3. component alone mainly (medio-)dorsally. Considering all movement components, the tip of the cercus-hook is moved (latero-)dorsally. So the hook of the cercus is moved towards a position in which it would lie in a horizontal (= frontal) plane of the body, but it is stopped in between by the structure Cst (Fig. 4), which bangs against the tergum: the hook of the extremely spread cercus points (ventro-)medially.

The effect of the opening movement of the cerci on the lamina accessoria+epiproct-element, which is suspended via two joints $j\ la-t$ to the tergum, is a caudo-dorsal rotation of the lamina accessoria+epiproct (as a unit) around a hinge joint axis running through the two joints $j\ la-t$, which is superimposed by a ventral movement of the epiproct in the $j\ e-la$. This results at all in almost no dorso-ventral rotation of the epiproct-tip, which is mainly displaced in parallel caudally.

With respect to the paraproct, the mC2-effect is a movement of the joint $j\ c-p$ caudally, together with the dorso-lateral edge of the paraproct. During this movement the paraproct is ventrally braced in its joint $j\ p_2-t_2$, which is the single concrete joint of the paraproct to the tergum. The paraproctal prong is moved mainly ventrally. This movement can be modified by superimposition of a lateral component, if the muscle mP2 also contracts; this should happen every time when the cercus+paraproct-system has to be opened far, before and after the male's grip onto the female.

Since the joint $j\ c-p$ is situated in *E. fatime* far laterally (in comparison to other Calopterygoidea, Figs 11e-f) and since the joint ($j\ p_1-t_1$) is not a definite joint any more, the range of mobility of the cerci and paraprocts apparently is enlarged secondarily.

The different components of the movement of the cerci – including the rotation-component around the longitudinal axis – seem to be useful for the movement of the cerci (which represent robust hooks with a complicated shape) out of the cleft behind the female pronotal lobe (Figs 13, 14 and below), when the male releases the female.

These components should also be essential in the reverse action, i.e. when the cerci grip the female pronotum: During clasping the strong main closer muscle mC1 (Fig. 4: mC1a, mC1b) will produce reverse force-directions of all movement-components described above. Its total effect is therefore correspondingly complicated. It is different compared to other calopterygoid and lestoid Zygoptera and will now be described in further details and in its correlation to the concrete linkage of the male to the female.

According to close-up photographs (made in Turkey, near Antalya, June 2000) the linkage between the male and the female of *E. fatime* has been reconstructed and tested by mountings of freshly killed animals (Figs 13, 14). The linkage is peculiar in several aspects:

The paraprocts are not involved in gripping. They only touch the dorsal surface of the female's pronotum not far caudo-laterally of the hole of the frontal apodeme of the prothoracic dorsolongitudinal muscles. Grinding traces in the epicuticle of the female pronotum, in the region where the paraproctal prong-tips contact the tergum, indicate variations in the gripping power of the muscle mC1 and/or translatory movements of the female in relation to the male during flight actions.

The cerci, while clasping, are spread very far dorso-laterally (Fig. 14a). The ventro-lateral rim of the posterior lobe of the female pronotum (lr, Fig. 13) is gripped by the (smaller) lateral hook of the cercus (lh) from laterally, while the distal main hook of

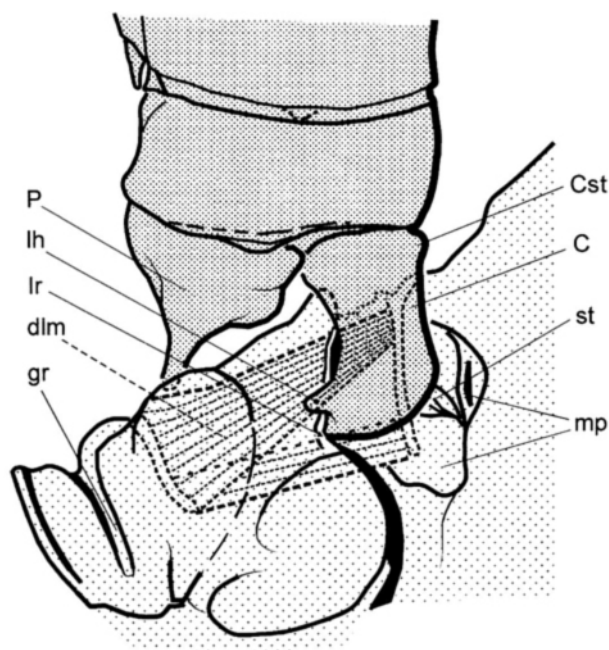


Figure 13. Tandem linkage in *Epallage fatime* — Cst: cercal stop; dlm: dorsal longitudinal muscle of the female between pro- and mesothorax (for its function in 'clamping the male', cf. text and also Fig. 14c); gr: groove of the anterior lobe of the female pronotum; lh: lateral hook of the cercus; mp: mesostigmal plate; st: stigma; lr: lateral rim of the posterior lobe of the female pronotum; further abbreviations see p. 131

the cercus extends behind the female pronotum (ventro-)medially; this position is similar to the extremely opened position of the cerci (see above).

The different force-components of the muscle mC1 in this linkage should mainly cause (a) the holding of the female from the side, by pressing the lateral hook of the cercus (lh) with an oblique fronto-mediad force against the ventral edge of the lateral rim of the posterior lobe of the female pronotum (lr, Fig. 13) and (b) the fitting of the large hook of the cercus into the cleft between the female's pro- and mesothorax, pressing the pronotal lobe from behind mainly in the *frontal* direction (= ventral direction with respect to the male); since there is no opponent force from the paraprocts (see above), this force seems to be useless (for its significance and for a possible accessory clasping force applied by the female, see below).

The dominant ventrally directed force component of the cercus-hook (with respect to the male's last abdominal segment) is directed forward, i.e. 'in flight direction' of the pair. Instead in other Calopterygoidea and Lestinoidea (e.g. *Calopteryx virgo*, *Lestes sponsa*) the dominant force component of the closing cercus is directed in a transverse section plane of the pronotum. This force component is certainly also present in the case of *E. fatime*, however not alone. The cerci of *E. fatime* seem to be able to grip the female

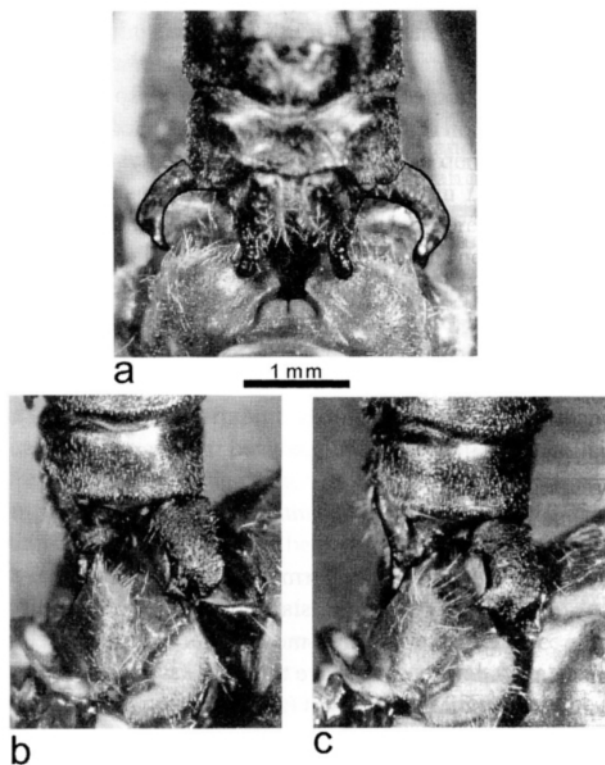


Figure 14. Tandem linkage in *Epallage fatime* — (a) frontal view; (b) and (c) lateral views. Parts of dead animals assembled according to close-up photographs. In (c) the female clamps the cerci of the male.

without an accessory grip of the paraprocts, mainly on account of the lateral grips of the lateral cercal hooks (lh) and their oblique forces. The force applied via the large cercus-hook seems to be necessary during strong pulling-flights of the male or when the male must act against resistance-actions of the female. Normally however this force seems to have no opponent force which could explain the presence of such a large hook.

Is a linkage via the cerci alone strong enough to keep the female attached also during extreme flight actions? At the rivulet in Turkey the newly coupled pairs moved away quickly at once, ascending high into trees. During these very quick flights the males obviously exert much pull onto the female. When coming back to the water, the couples showed curious vigorous up-and-down flights, during which the female's abdomen repeatedly dipped the water surface. It looked just like egg-laying of libellulids. Egg laying however is executed afterwards in the normal zygopteroid way. Therefore this 'surface dipping flight' might be some kind of testing the water by the female. One can expect that the linkage between the partners will be stressed very much during these vigorous up and down flights. In this context, however, an interesting aspect attributed to the special tandem linkage of *E. fatime* should be mentioned: Since the main hooks of the cerci are placed in the cleft between the female's pro- and mesonotum, the female is able to clamp the cerci by contracting her dorsolongitudinal tergal muscles (dlm, Fig. 13) and closing the intersegmental cleft (Figs 14b-c). More precisely, the cerci can be clamped by special lateral structures of the mesothoracic front (mp, Fig. 13). This should make the linkage more stable in moments when it is necessary.

Can this special combination of features in the male clasping apparatus and tandem linkage of *E. fatime* be estimated to be close to the mentioned theoretical starting-point of a transition towards the anisozygopteroid-anisopteroid systems? The spatial relation between the cerci and epiproct+lamina accessoria in *E. fatime* is indeed already such that an EMR, which would couple the functions of the epiproct+lamina accessoria and the cerci as in Anisozygoptera + Anisoptera, seems to be 'not far away'. *E. fatime* seems to be in a preliminary stage for EMR, since only small changes are necessary to make the epiproct move in an anisozygopteroid-anisopteroid (= 'senseful') way in combination with the cerci. A further indication is that a linkage shifting from the pronotum to the head can be easily reconstructed theoretically starting from an epallagoid linkage – without an obvious weakening of the tandem-stability during this shifting. These evolutionary steps of EMR and linkage shifting will be analyzed in the next chapter.

EMR, linkage shifting and further transformations

Figures 15a-d show the hypothetical transformation of a rather normal zygopteroid (pre-epallagoid) system (a) via an intermediate state (b) to an epallagoid (c) and post-epallagoid system (d). At first only the opening-movements are considered.

When the muscle mC2 contracts to move the cerci laterally relative to the paraproct in the joint j c-p in the pre-epallagoid system (a) the epiproct is lifted (= rotated dorsally) mainly as a lamina accessoria+epiproct-unit around a hinge joint axis la-t/la-t (indicated only in a), and is also lifted to a small extent in the joint j e-la relative to the lamina accessoria. These dorsad rotations are due to the fact that the point of the cercus which produces a lever effect is positioned ventral of the epiproct. The paraproct is illustrated as

to open at the same time (together with its paraproctal prong which is not indicated) by contraction of the muscle mP2; since the joint j c-p is moved caudo-laterally by this, also an indirect opening effect is transferred from the paraproct to the cercus (as described for other zygoterans).

In Figure 15b the relations between the cerci and the lamina accessoria+epiproct have changed with respect to the place where the cercus-leverpoints meet the lamina accessoria+epiproct. Furthermore the muscle mC2 became (weakly) oblique. These alterations must have led (1) to the addition of a dorsal component to the lateral movement of the cercus and (2) to a (beginning) rotation of the cercus around its longitudinal axis. Regarding the movement of the lamina accessoria+epiproct, caused by the opening of the cerci, there is no fundamental change, but the movement is diminished on account of the diminished lateral component of the opening-movement of the cerci and the shortened lever between the cercus-leverpoints and the axis la-t/la-t. With respect to the epiproct alone there is now a *ventral* movement in its joint j e-la, since it is its dorsal margin which is now moved caudally, when the cerci open. This movement is small at this state (and is therefore not indicated in the Fig.), since the membranous zone ventral of the epiproct gives enough clearance for the movement of the lamina accessoria+epiproct as a unit.

Figure 15c (the epallagoid state) in this respect is more advanced. Since the lever-effect to the axis la-t/la-t is again diminished – and the joint j e-la again plays a role for a certain ventral epiproct-movement – an at all approximately neutral action of the epiproct is assumed (cf. also Fig. 11f).

As soon as the membranous area ventral of the epiproct is shortened (Fig. 15d; for reduction of the lamina supraanalis and further alterations, see below), the caudal movement of the joint j e-la during the opening movement of the cerci will lower the epiproct (= rotate the epiproct-tip downward) more strongly from that moment on, in which the ventral membrane is stretched, whereas the lamina accessoria is lifted around la-t/la-t as before. Now the EMR fundamentally has taken place.

The muscle mLa2, extending in *E. fatime* from the lamina accessoria to the tip of the lamina supraanalis (Fig. 15c), reversed its origin- and insertion-point during the transformation c→d: In (c) the mLa2 is a thin long muscle, the function of which is to lift the lamina supraanalis, a membranous lobe, cushioning the anus from dorsally – since the lamina supraanalis forms a trough, the movability of the lamina supraanalis might be mainly essential for the dispersion of the secretion of the epiproctal gland in the Zygotera. In (d) the lamina supraanalis is reduced in size and the muscle mLa2 – the ventral insertion-points of which have been translocated dorso-laterally – is now able to contribute to the ventral (= opening-) movement of the epiproct as well as the opening-movement of the cercus (precisely: its lateral component) by moving the joint j e-la caudally. The principle of this effect is the same as described for *A. cyanea* (Fig. 10): it is the caudad movement of the joint j e-la between the lamina accessoria-tergum-hinge and the ventral attachment region of the epiproct, which effects the lowering of the epiproct. The ventral attachment of the epiproct functions like a ribbon, which is stretched mainly in the extreme ranges of the movement. The effects of the muscles mLa2 and mC2 in opening the cerci and lowering the epiproct are now mutually strengthened.

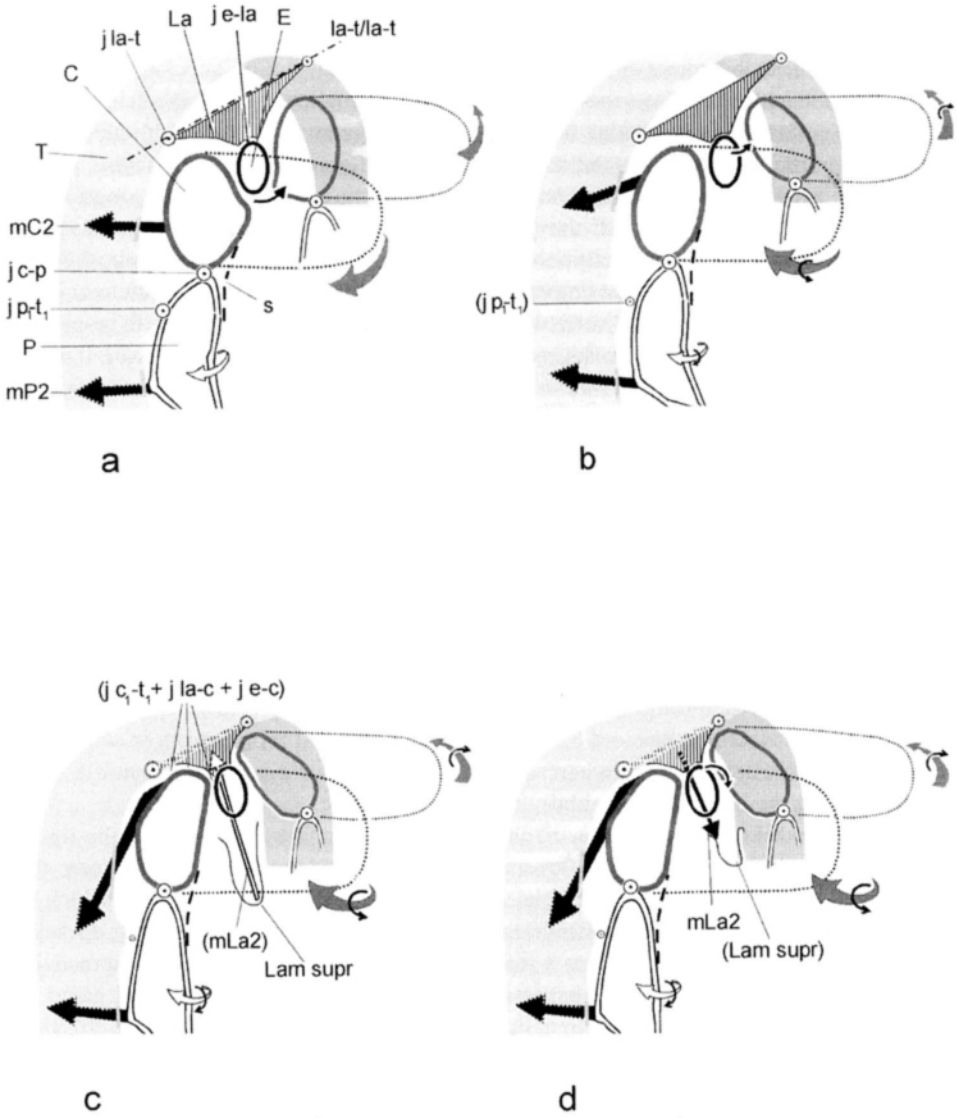


Figure 15a-d. Epiproctal movement reversal (EMR) — (a), (b) pre-epallagoid states; (c) epallagoid state; (d) post-epallagoid state (grip 2* in Figs 17, 19). For details see text. Only the opener muscles of the cercus, paraproct and epiproct (and respective movement-arrows) are indicated. Lamina supraanal and muscle mLa2 are illustrated only in (c) and (d). — \odot point-joints with ball joint-like characteristics; s: ligamentous connection between cercus and paraproct; la-t/la-t: hinge joint axis running through the joints j_{la-t} of both sides (indicated only in a); further abbreviations see p. 131.

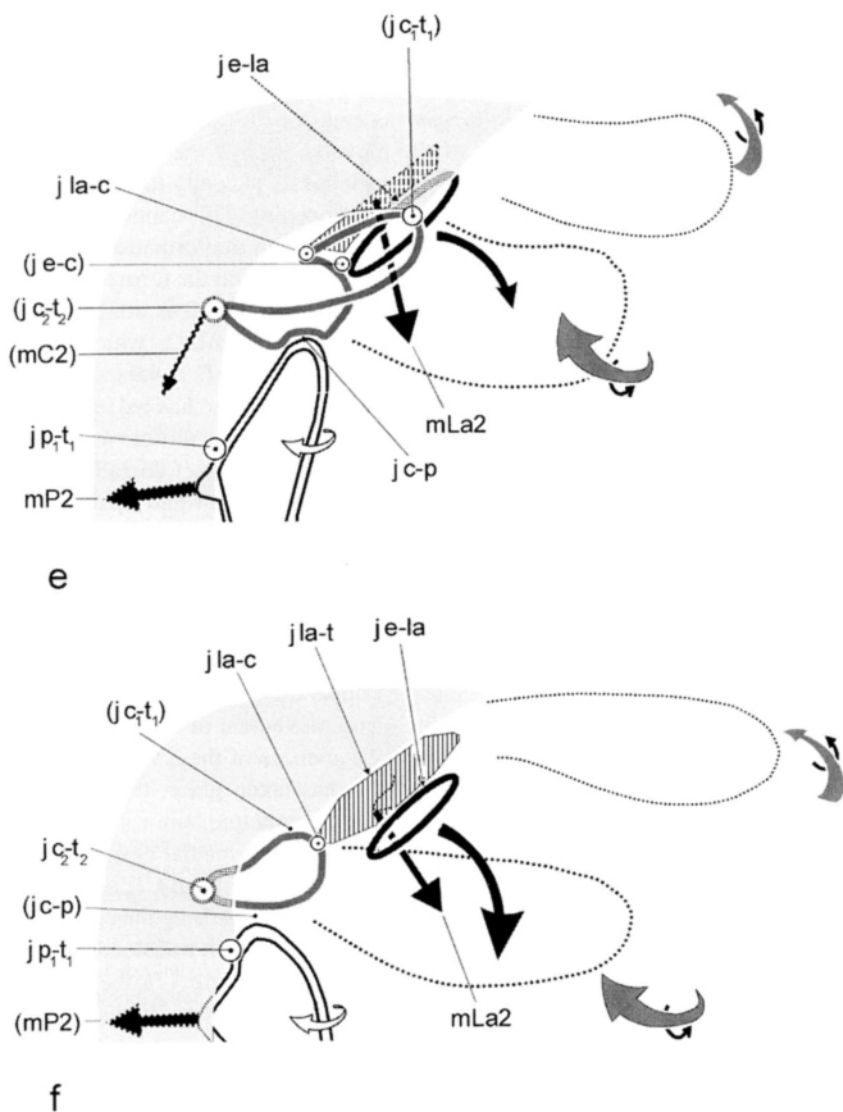


Figure 15c-f. Extant 'outcomes' of the EMR — (e) anisozygopteroid and (f) anisopteroid state. The main elements of the male clasper apparatus (cercus, paraproct, tergum, lamina accessoria, epiproct) are depicted as in Figures 15a-d, but not specifically labeled. The proximal outline of the cercus in (e) has been exaggerated to show all essential relations to the tergum, paraproct, lamina accessoria and epiproct; the 'joint' ($j_{c_1-t_1}$) e.g. is situated far caudally on account of the caudad protruding medial portion of the tergum (Figs 5, 6). For changes in structure and function see text. Abbreviations see p. 131.

There exist two means to establish a functional reversal of the muscle mLa2, which seem to have been used both in the stem group of the Anisozygoptera + Anisoptera and then within this group: (1) To shift the ventral mLa2-insertion points to the latero-dorsal borders of the lamina supraanalis-evagination, thus separating the left- and rightside muscles ventrally (for the primitive situation in which the mLa2 converge ventrally, see Fig. 16). The pull of the muscles is now concentrated to the side walls of the anal opening, more distant from the region of the movable part of the lamina supraanalis. (2) To shift the ventral insertion-point of the muscle mLa2 caudally towards the (sclerotized) ventral edge of the epiproct, away from the anal opening. This happened presumably in the stem group of the Anisoptera and was correlated with the formation of a (secondary) direct articulation of the lamina accessoria to the tergum and the formation of a larger lever-like structure on the lamina accessoria to which the mLa2 is attached dorsally. These alterations led to an increased effect of the muscle mLa2, which moves the epiproct now mainly ventrally, instead of ventro-caudally as in *E. superstes*.

Regarding the closing of the clasp apparatus, the EMR also has led to an alteration of the functional co-ordination of the involved muscles: When the muscle mC1 contracts, the forward movement of the cercus-leverpoint rotates the epiproct dorsally (= closing) in the post-epallagoid state – in contrast to the pre-epallagoid and epallagoid states (Figs 15a-d, movement-arrows reversed). The muscle mC1 and the muscle mLa1 are both able to manage this in the post-epallagoid state (d), since both muscles cause a frontal movement of the dorso-medial leverpoint of the cercus and a frontal movement of the joint j e-la. This means that the muscles mC1 and mLa1 have been synchronized as synergistic closer-muscles. They mutually strengthen one another (just as the opener muscles in the case of the opening of the clasp apparatus, see above) – with respect to the lifting-movement of the epiproct and the closing-movement of the cercus.

We should consider now the evolutionary consequences of the EMR for the specific linkage between male and female. After the EMR has taken place, the male clasp apparatus is capable of using the epiproct as a gripping structure, since a dorsal (= closing-) movement of the epiproct is co-ordinated with a ventro-medial closing-movement of the cerci. Both movements are effected by the strong muscles mC1, assisted by the muscle mLa1. With respect to a future possibility of a linkage-shifting the epiproct works in the 'correct' way on the 'correct' side of the cerci – it has been translocated relatively to the cerci in the direction of the head of the female. In Figure 17a the hypothetical tandem linkage of such a constellation is illustrated. This Figure shows a post-epallagoid clasp apparatus (already standing in the evolutionary line which led to the Anisozygoptera + Anisoptera), for which it is assumed that the cerci were linked to the female's pronotum just as in *E. fatime* (Figs 13, 14). In contrast to *E. fatime* however the EMR has taken place and the epiproct is already slightly involved in gripping, since it is pressed against the caudal elevation of the female's pronotum in the dorsal direction (with respect to the male). This dorsal pressing of the epiproct, effected by mC1+mLa1-contraction, opposes the strong ventral force-component applicated through the cercal hooks during closing, which presses the female pronotum from caudally (cf. *E. fatime*). In early stages the clasp apparatus could have been assisted e.g. by a suction-effect of a distal membranous surface of the epiproct and/or by the secretion of the epiproctal gland.

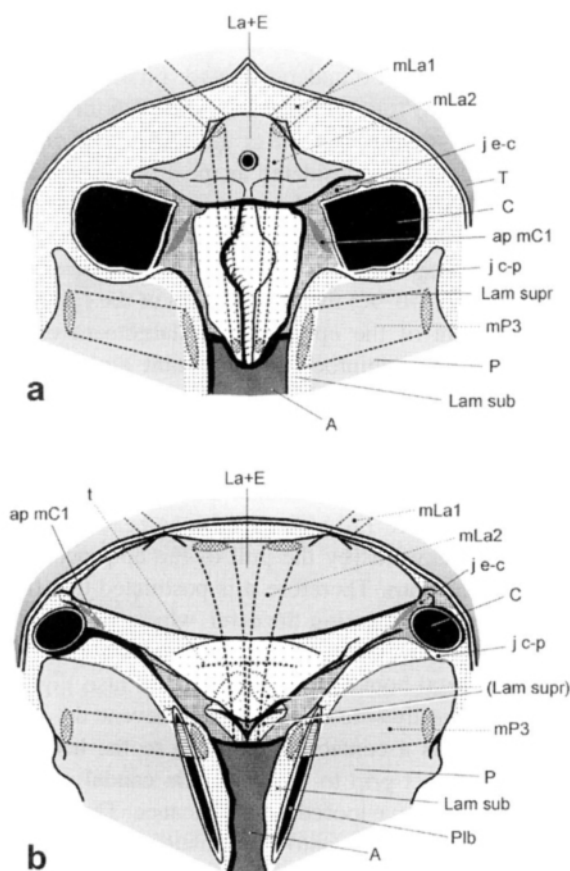


Figure 16. Last abdominal segment of female (a) *Epallage fatime* and (b) *Epiophlebia superstes*; caudal view. The dorsal joint of the cercus (j e-c) is designated according to the adjoining part of the composite element lamina accessoria+epiproct. — In *E. fatime* the epiproct is rather small and shows the typical gland orifice of the Zygoptera; the lamina supraanalis forms a trough and is presumably engaged in the dispersion of the gland secretion (as in the males). In *E. superstes* small folds beneath the membranous epiproctal tip, which extend to the anal opening (A) are interpreted as remnants of the lamina supraanalis showing still zygopteroid features (and supporting the direction of evolution as described). Accordingly the tip of the female epiproct is interpreted as a secondary structure, evaginated between the lamina accessoria+epiproct and the lamina supraanalis (corresponding in place the new epiproct-enlargement of the male). The epiproct+lamina accessoria and this membranous tip together form a triangle, resembling a 'normal', orthopteroid epiproct; this aspect however is 'accidentally', since it has been acquired secondarily via addition of a new part. The paraproctal lobe (Plb) is cut proximally. Since the muscle mP3 crosses the base of the Plb, the Plb theoretically could represent the paraproctal prong; however, occurring as well in males as in females of *E. superstes* (instead the paraproctal prongs occur only in males in the Zygoptera), it is more likely that it is a newly formed structure, evaginated from the lateral region of the lamina subanalis. The lamina subanalis is represented (in males and females) by a membranous region medial of the paraproctal lobe; the muscle mP3 is inserted to the lateral edge of it. Dashed line (t) indicates the (hidden) turning line, where the ventral (=frontal) cuticle of the membranous epiproct-tip merges into the wall of the lamina supraanalis-remnant. — apmC1: apodeme-invagination of muscle mC1; further abbreviations see p. 131. — In the female of *Aeshna cyanea* the aspect of the epiproct (+lamina accessoria) is similar to *E. superstes*. The lamina supraanalis however here represents an evagination of the ventral side of the epiproct, corresponding to that of the male (Fig. 9). For Plb and paraproctal prong-vestige in males of *A. cyanea* (the latter occurring only in males), cf. Figure 9a.

The problem of the integration of a new, unpaired, medially-situated structure into the clasping apparatus should not be underestimated. First: The epiproct had to begin as a small structure. Second: At this state the gripping-point of the epiproct must have been situated near to the cross-sectional plane of the cercal grip, only slightly in front of it (with respect to the female). It is considered as most essential – mainly in this initial situation – that the (epallagoid) cercal hooks already extended far medially, behind the female's pronotum. Only in that way the cerci could have been useful as opponent structures to a newly formed epiproct, which worked mainly in the mediosagittal plane.

By getting larger (Figs 17a→b→c) the participation of the epiproct was successively enhanced via an enlargement of the epiproct (= enlargement of the working lever) and frontal translocation of the epiproct-clasping-point along the female pronotum. The touch of the epiproct-tip with the female's head (a little past Fig. 17c) was followed by complete transfer of the epiproctal grip to the head (17d). This 'evolutionary jump' to the female's head seems to have been only an organic further step in evolution. However it was an ambiguous step, as well in functional respects as concerning the following grip-shifting. The arrows in Figure 17d indicate that the head of the female in this state should have been rotated backwards by the pull of the epiproct. This however would have been clearly disadvantageous. Therefore it is postulated that further modifications of the male clasping apparatus concerning the cerci, which prevented this head-rotation, must have been evolved at the same time. This could have been achieved as illustrated in Figure 17d, where the lateral hooks of the cerci (lh; cf. also Figs 4, 13) are enlarged – e.g. to secure the grip laterally – and are able to prevent the caudal head-rotation. As soon as this stop, which is a contact of the cerci to the head, had been acquired in combination with an epiproct-grip to the head, the caudal grip of the cerci to the pronotum automatically should have loosed its significance. The main step of the shifting of the whole male clasping apparatus onto the female's head was now accomplished and the prothoracic grip of the cerci could be abandoned completely.

Figure 17d shows that the epiproct was anchored to a caudal ridge on a zygoteroid female head, because this type of dorso-ventrally flat head can be estimated as most suitable for the shifting of the epiproct.

In the row Figures 17a→d it is indicated that the paraprocts, the function of which is already negligible in *E. fatime*, progressively have been reduced in size. This 'synchronized' reduction however is hypothetical. The reduction of the paraproctal prongs need not necessarily be correlated to the enlargement and shifting of the epiproct. Therefore, if e.g. certain fossils exhibit a larger paraproct (= paraproct with a paraproctal prong), these fossils will not have to be automatically classified as "zygoteroid". To substantiate the question whether to classify fossils as zygoteroid or as transitional within the stem group of Anisozygoptera + Anisoptera, one should at least be able to verify the actual size of the epiproct. Lohmann (1996: 218) e.g. supported his theory of a supposed linkage shifting with arguments concerning a different equipment of the clasping apparatus in the fossils *Tarsophlebia* and *Stenophlebia*. *Tarsophlebia*, however, according to the above considerations, could have been already transitional or it could even represent a later state.

Now the question arises whether it is likely that the paraproctal prongs were involved in the clasping in the transitional phase. The theoretical possibility that a 4-part-grip,

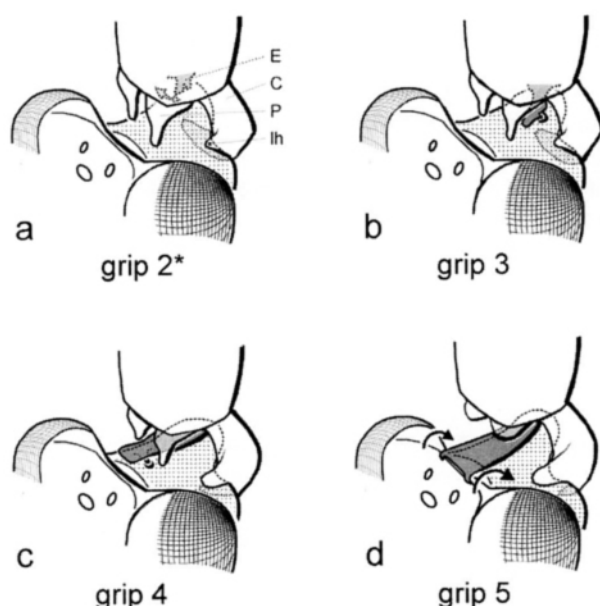


Figure 17. Tandem linkage shifting — reconstruction of the evolution of the tandem linkage from a post-epallagoid state (a, grip 2*) to a state lying previous to the common ancestor of Anisozygoptera + Anisoptera (d, grip 5); cf. text and Figure 19. — Female pronotum punctuated; lh: lateral hook of the cercus; further abbreviations see p. 131.

in which the cerci and the paraprocts are actively collaborating, had been shifted during evolution from the caudal end of the female pronotum towards its frontal end, can be evaluated as less likely, since a newly evolved epiproct would have to be co-ordinated in function to a 4-part-grip. In a linkage performed by a 4-part-grip the cerci would work mainly in a cross-sectional plane. The epiproct, which works mainly in the medio-sagittal plane, would have difficulties to evolve. A possibility to allow a functional co-operation of the epiproct with a 4-part-grip could theoretically exist, if the paraproctal prongs alone would shift forward along the female pronotum and come to grip the anterior rim of the female prothorax — the cerci and the paraproctal prongs then working against one another in mainly sagittal planes. However, there is no obvious reason why this type of an attachment on the female should have been abandoned by replacing the paraproctal prongs with the epiproct (which is very small initially).

There is also no indication that other types of specialized zygopteroid 4-part-linkages could represent a starting point of an evolution towards the Anisozygoptera + Anisoptera. For instance in species (e.g. *Coenagrion puella*; for further species see Jurzitza 1974), in which the hind margin of the female pronotal lobe is gripped by pressing the cerci and paraprocts (on each side of the body) from both sides towards the lobe (the ipsilateral cercus and paraproct working towards one another), the paraprocts are really indispensable. Again there is no need for a further structure — and no possibility is obvious for a new structure to oppose the cerci during gripping.

Therefore the paraprocts which indeed could have been preserved with a relative long paraproctal prong for quite some time (see above; for the supposed paraproctal prong-vestige in *A. cyanea*, cf. Fig. 9) presumably did, already in an early state, not use the paraproctal prong as a gripping structure any more, resembling the situation in *E. fatime*. The ability of *E. fatime* to grip the female solely with the cerci is evaluated – in combination with other features – as a strong argument in the identification of its clasping apparatus as a model of a ‘starting point’.

Continuing the grip-shifting series as outlined in Figures 17a-d we will come to the extant linkage-systems of Anisozygoptera and Anisoptera. Figures 15e-f illustrate some of the fundamental acquisitions of Anisozygoptera and Anisoptera concerning the male clasping apparatus diagrammatically, using the same style as in Figures 15a-d. In Anisozygoptera (*E. superstes*) the formerly simple base of the cercus (Fig. 15d) has been largely changed; to show all the essential connection-points of the cercus in a two-dimensional drawing it was necessary to ‘distort’ the morphologic reality to some extent. On account of the movement of the whole kinematic system and the special attachment of the cercus to the tergum (existence of an oblique movement-axis $(c_1-t_1)/(c_2-t_2)$), the opening-movement of the cercus shows a dorsal and a lateral component, combined with a rotational component around the longitudinal cercus-axis. Compared to *E. fatime*, the dorsal and lateral components are similar, the rotational component however is contrary. In the mechanical working model of the clasping apparatus of *E. superstes* (Figs 7, 8) the function of the complex attachment of the cerci could be simulated by incorporating a single tergo-cercal ball joint on each side, showing that no membranous play of the cerci is needed in principle. But presumably those movement-clearances, which in fact are present, allow *E. superstes* to spread the cerci and epiproct to a greater extent and also allow larger left-to-right side-differences of movement.

The joints j la-c are only weakly able to transmit force between the lamina accessoria and the cerci in *E. superstes*. Therefore the joint-like connections (j e-c) seem to be essential in supporting the joints j la-c: the cerci of both sides are coupled more strongly via this ‘double-articulation’ to the lamina accessoria+epiproct-system. The existence of the (j e-c)-connection has as a consequence a close proximity of the cerci to the proximally broad epiproct. This is probably a primitive feature of the Anisozygoptera + Anisoptera. Regarding the evolution of the main closer muscle mC1, this proximity of cerci and epiproct has been essential, since it allows a shift of the mC1-insertion from the cercus-base to the base of the epiproct in the stem group of the Anisoptera. Because of the small lever of the muscle mLa2 and the membranous clearance between the cerci+lamina accessoria and the tergum in *E. superstes*, this system of changing the angle between the lamina accessoria and epiproct in the joint j e-la seems to be less efficient compared to the Anisoptera. Therefore the muscle mP2 is presumably necessary in *E. superstes* to support the muscle mLa2 in opening the cerci and the epiproct.

A system in which the cerci need not open in such a complicated way as in *E. fatime* – but are opened efficiently from the lateral direction via the muscle mP2 and from the medial via mLa2 (the new opener muscle) – does not need a muscle mC2 any more. Therefore the muscle mC2 was reduced, presumably at the base of the Anisozygoptera + Anisoptera. It is interesting that in *E. superstes* a thin rudiment of the muscle mC2, which

extends very obliquely from the lateral edge of the cercus ventro-latero-frontally to the tergum (Figs 5, 6, 15e), could be found in some, presumably pre-adult males.

In summary there are several indications for the assumption that *E. superstes* represents a necessary intermediate transition stage on the way to the Anisoptera and cannot be estimated as an autapomorphous side branch: (1) the essential role which the paraprocts already play as lateral suspensory elements of the cercus-lamina accessoria+epiproct-system, (2) the oblique mC2-vestige, which indicates the existence of antecedents which moved the cerci in an epallagoid way and (3) the proximally broad epiproct. However the paraproctal prong has been reduced totally in this evolution-line – the membranous outgrowth “Plb” of the paraproct cannot be homologized with the paraproctal prong (cf. legend to Fig. 16).

The finding of the correct places of the epiproctal grip-structures at corresponding places on the female's head has been described as to be to a far extent ‘automatic’ in the Anisozygoptera + Anisoptera. The epiproct in *E. superstes* grips the head of the female with its lateral hooks at the place where the furrows between eyes and postfrons end (“copulatory sockets”, Asahina 1954). This place is situated already near the postfrontal suture, where the epiproct primarily should have been attached in antecedents (Fig. 17d). In Anisoptera there are epiproct-grips to different places of the female's head (e.g. Pinhey 1969). Grip-shiftings within Anisoptera with respect to the female head are fundamentally comparable to the shifting of the epiproct along the female pronotum in the stem group of the Anisozygoptera + Anisoptera. Every step of these grip-shiftings should have been initiated by a double grip. This means that the tip of the epiproct must have primarily touched and then gripped the points which lie more distantly, while the former grip was still working; afterwards the former grip could be reduced. In this way the epiproct must have ‘climbed’ a considerable distance during the evolution within the Odonata, from the posterior end of the pronotum to the antefrons of the head (cf. the figure of e.g. *Onychogomphus forcipatus* (Linnaeus), Robert 1959: fig. 14).

To illustrate the situation within the Anisoptera, the clasping apparatus of Aeshnidae is diagrammatically illustrated in Figure 15f. This system shows some highly apomorphic features. The functional co-operation of the cerci and lamina accessoria+epiproct e.g. got largely independent from the paraprocts (only in *O. forcipatus*, a species with a very large grip-span, could a secondary suspension be found between the epiproct and the paraproct). There is no concrete joint j c-p between the cercus and paraproct any more. Furthermore the joint j c₂-t₂ has been established as a very concrete and essential antero-lateral joint of the cercus, sometimes (e.g. in *A. cyanea*) lying in a highly differentiated ‘pocket’ of the tergum. The movements within this joint are strongly limited by stops arranged caudally of the joint between the cercus and the tergum. The cerci have now a diminished role compared to the epiproct, since the muscle mC1 is secondarily inserted directly to the epiproct-base (Fig. 9). Furthermore the epiproct became proximally small and reduced its lateral joint-connections to the cerci. This was possible after the mC1-insertion had shifted to the epiproct and after the weak epiophlebioid joint j la-c (see above) had been strengthened.

The lamina accessoria is articulated directly to the tergum – just as in *E. fatime*. However if the apparatus of *E. superstes* is transitional (see above), this hinge joint of

the lamina accessoria to the tergum presumably represents a derived (= convergent) feature and not a primitive one.

This evaluation implies that the joints j_{la-t} – which are weakly represented in *E. fatime*, suspending a weakly sclerotized lamina accessoria to the tergum – have been reduced in a post-epallagoid = pre-epiophlebioid state (between Figs 15d and e). *E. superstes* shows a system in which both the span of the cerci and the epiproct are still large – on account of the membranous clearance between the cerci+lamina accessoria and the tergum, which permits a considerable backward translocation of the cerci and epiproct (omitted in the mechanical working model; Fig. 7). This large span of the cerci and the epiproct should have also been present in all states of grip-shifting (Figs 17a-d). The accentuation of the function of the epiproct (mC1-shifting, mLa2-lever-enlargement) in the stem group of the Anisoptera then evolved at the expense of the cercus-span and active movability. The primary suspension of the cercus-lamina accessoria+epiproct-system via the paraprocts has now been replaced by new suspensions of the cerci (joints $j_{c_2-t_2}$) and the lamina accessoria (secondary joint j_{la-t}).

As a consequence of the direct lamina accessoria-to-tergum-articulation the direction of the epiproct-movement has changed (Figs 15e-f, 10). Furthermore the opening of the epiproct has been made more efficient through a large lever-apodeme on the lamina accessoria (Fig. 9) and through a caudad displacement of the ventral insertion-points of the muscles mLa2.

The whole system of *A. cyanea* may be characterized as a secondarily simplified one. It is interesting that the movements of the lamina accessoria+epiproct are not 1:1 transferred to the cerci – partly on account of the fact that the cerci are hard to move in the joints $j_{c_2-t_2}$ and partly on account of a distortable lamina accessoria. This trend has been continued in other groups of Anisoptera – obviously convergent in several families: In *Somatochlora metallica* (Vander Linden) e.g. the lamina accessoria+epiproct became totally independent from the cerci, since the joints j_{la-c} have also been reduced. Thus the cerci, which are attached elastically (only with a very small movability) to the tergum, represent the opponent claspers of the epiproct without having an own active mobility. There is indeed no more muscle force that could move the cerci to oppose the antero-dorsal movement of the epiproct. The contraction of muscle mC1 moves only the epiproct, forcing the female head against the male cerci, which immediately attain their extreme (= 'opened') position. The head is clamped effectively between the epiproct and the cerci only via the pressure of the epiproct.

So, seen in an overview, the clasping apparatus of the Odonata has evolved from a zygoteroid system in which the lateral parts (cerci and paraprocts) are manipulated by own muscles, via a system in which lateral and medial claspers (cerci and epiproct) do both participate (*E. superstes*), to the anisopteroid system, in which mainly (only) the median epiproct-clasper is moved by muscles. The muscle mC1 shows interesting functional alterations during this evolution: it is a direct epiproctal depressor in the larvae, closing the whole anal pyramid; as a cercal (closer-) muscle in the imago of zygoterans it is an indirect depressor (' opener') of the (small) epiproct; it has been transformed to an indirect epiproctal levator in the stem group of the Anisozygotera + Anisoptera, again functioning as a closer of a system (the clasping apparatus – compared to the larvae moving the epiproct in the opposite direction); after its shifting it became again a direct epiproctal muscle.

Phylogenetic implications and outlines of evolution

Indications for paraphyly of Zygoptera

Pfau (1971) suspected that the zygopteroid secondary male copulatory apparatus has been modified at the base of the Anisozygoptera and Anisoptera into structures that work more efficiently while changing flight and the zone of activity from the shore regions to more open water regions. The 'slow' zygopteroid copulatory apparatus, as well as the special zygopteroid type of flight apparatus, seem to have been insufficient in the new ecological zone. A similar aspect could have played a role in the case of the clasping apparatus, which is even easier to understand.

Comparing the flight apparatus and the wings of different groups (including fossils) Pfau (2000) came to the conclusion that the evolution probably led from the zygopteroid flight apparatus – with petiolate wings with a proximal nodus – to the anisozygopteroid-anisopteroid flight apparatus and that Fraser's hypothesis (Fraser 1954, 1957) that certain Zygoptera ("Lestine Complex", Calopterygoidea) are offshoots of the phylogenetic branch which led to the Anisozygoptera + Anisoptera might be correct (this means a paraphyly of "Zygoptera" – in the sense of Hennig 1966, 1969). Fraser's hypothesis, which was based mainly on morphological characters of the wings, has been reviewed using correlated characters of the functional morphology of the wings and of the thoracic wing driving apparatus. This led to some indications of support for principal parts of Fraser's hypothesis. Now the results presented here, which are deduced from the comparison of the clasping apparatus of different groups, also point in this direction: the possibility to reconstruct an evolution without functional gaps from an epallagoid to an anisozygopteroid-anisopteroid linkage indicates that *Epallage fatime* may stand near to the starting point of the EMR plus linkage shifting. However, further arguments will be necessary to exclude (or to support) the possibility of an accidental situation (in the case of the clasping apparatus) or of a convergent evolution (in the case of Fraser's characters of the wings).

It is useful, therefore, to try to determine some of the characters of the flight apparatus and wings more precisely, to find parameters for their evaluation which can be measured more exactly. There are three parameters that should be considered in this context:

- (1) The basic angle of wing stroke-plane. This parameter has been determined indirectly in mediosagittal sections through animals by measuring the angle of the wing upstroke muscles (dvm, Fig. 18c) between a line through the muscles and a line through the metapoststernum. The direction of the dorsoventral power muscles, which should be most essential for at least the path of the upstroking wings, is designated here as the 'basic angle of wing stroke-plane'. Influences of other muscles – which are more or less contracted in fixated animals – however could not totally be excluded by this method. The outcome of this determination is that zygopteroid odonates ("precision-manoeuvre fliers", Pfau 1986, 1991) show a smaller basic angle of wing stroke-plane than Anisozygoptera + Anisoptera ("forward-thrust fliers"). That is, Anisozygoptera + Anisoptera secondarily shifted the angle towards the vertical, to acquire steeper wing strokes. This evolution shows transitional stages (cf. *Calopteryx haemorrhoidalis* [Vander Linden] and *E. fatime* in Fig. 18c). It is interesting that in *Epiophlebia*

superstes the wing stroke-plane, according to the angle of the dorsoventral muscles, must be very steep, exceeding even that of *Aeshna cyanea*. Most interesting is the difference in the angle of the wing stroke-plane between the fore- and the hindwings. This difference is large in *C. haemorrhoidalis*, *E. fatime* and the Anisozygoptera + Anisoptera compared to *Erythromma najas* and *Lestes dryas* Kirby. It presumably was not accidental that the basic angle of wing stroke-plane has been altered in the mesothoracic segment more than in the metathoracic segment, and not vice versa. Considering the aerodynamic co-operation of the two pairs of wings it seems clear that the aerodynamic effect of the forewings on the hindwings is greater than that from the hindwings on the forewings. During the strong forward flight it should therefore be disadvantageous if the forewings would change the direction of the airstream that meets the hindwings to a larger extent. So, the more vertical wing stroke in the mesothorax could be interpreted as adaptive.

- (2) Different capabilities to change the basic angle of wing stroke-plane. While the zygopteroïd system has preserved capabilities to change the angle of wing stroke-plane in the meso- and metathorax via two pairs of smaller muscles ("adjusting muscles" dlm and pa, Pfau 1986), the Anisozygoptera and Anisoptera have reduced these muscles more or less, mainly in the metathorax. Figure 18b compares the apodeme-length of the dorsolongitudinal muscles (dlm) in the two segments. This apodeme-length represents the operating lever of the dorsolongitudinal muscles (for different functions of the dlm in the meso- and metathorax, see Pfau 1986: 61f). In *E. superstes*, and much more in *A. cyanea*, the apodeme has been reduced in length in the metathorax, indicating a different specialization of this flight segment in comparison to the (primitive) zygopteroïd state. To describe this more exactly: according to the different functions of the dlm in the two flight segments, the mesothorax has kept its former ability to make the wing stroke-plane more horizontal while in the metathorax the ability to make the wing stroke-plane more vertical has been reduced. Figure 18b indicates that this evolution only concerns the Anisozygoptera and Anisoptera, but the Anisoptera much more than the Anisozygoptera.
- (3) The position of the nodus. Measurements of the position of the nodus in relation to wing length (Fig. 18a) show that *E. fatime* had already acquired an anisozygopteroïd-anisopteroïd state. Furthermore: a comparison of the fore- and hindwings shows that the position of the nodus is more different in *E. fatime* and the group Anisozygoptera + Anisoptera than in *E. najas*, *L. dryas* or *C. haemorrhoidalis*. The nodus-position is evaluated as an essential indication for wing differentiation, since (according to Pfau 2000) it indicates different degrees of a functional bisection of the wing into a proximal 'bearing-surface part' (specialized to produce mainly aerodynamic lift-forces) and a distal twisting part (specialized to produce mainly forward thrust-forces). This large difference between forewings and hindwings in *E. fatime* + Anisozygoptera + Anisoptera could be correlated to the different basic angles of wing stroke-plane of the thoracic segments (Fig. 18c): Since the wing stroke-plane is considerably steeper in the mesothorax – in certain calopterygoid groups (cf. *C. haemorrhoidalis*, *E. fatime*) and mainly in the Anisozygoptera + Anisoptera –, the more distal position of the nodus in the forewing could be interpreted as a means of producing a relatively greater proximal wing area which is

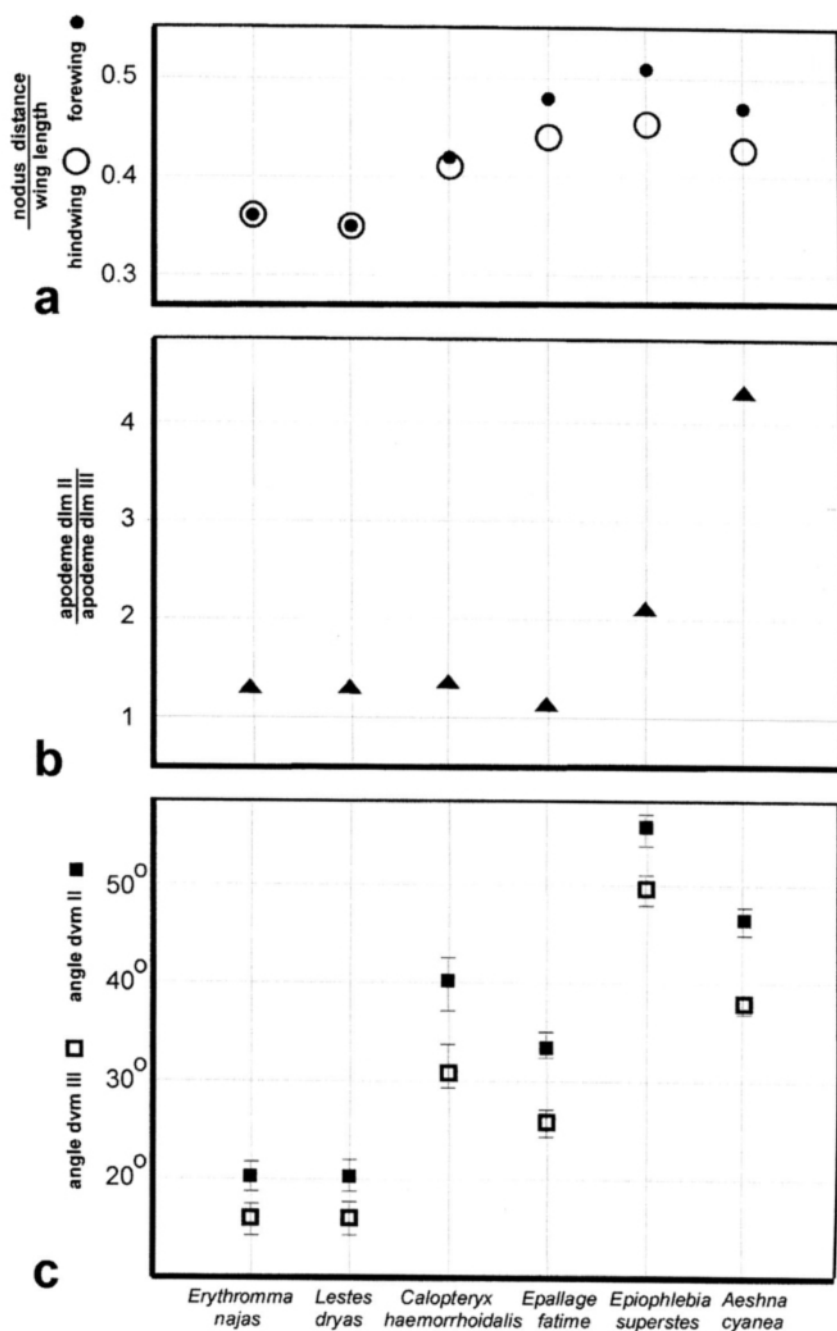


Figure 18. Flight apparatus and wings — characters supporting the (multiple) paraphyly of the Zygoptera (a and c) and the monophyly of the Anisozygoptera + Anisoptera (b); cf. text and Figure 19. — dlm: dorsolongitudinal muscles; dvm: dorsoventral muscles; II: mesothorax; III: metathorax.

specialized for lift production, to be able to counterbalance the more increased production of forward thrust of the forewings.

However there are further parameters which could play a role in the context of (3), e.g. the capability to change the stroke-plane in fore- and hindwings via the adjusting muscles dlm and pa, which are different in Calopterygoidea, Anisozygoptera and Anisoptera. It is worth mentioning, e.g., that the muscles dlm and pa are considerably smaller in *E. fatime* than in *C. haemorrhoidalis* – in spite of a relatively more voluminous thoracic flight apparatus in *E. fatime* – a possible synapomorphy with Anisozygoptera + Anisoptera. Furthermore there is a different degree to which the basal region of the fore and hindwing has been broadened, again to counterbalance deficits of lift production, which should be taken into consideration. The parameter ‘wing stroke-frequency’ – which is quite unequal e.g. in *Calopteryx* and *Epallage* – in any case should also play an essential role.

It is most interesting that the enlargement of the divergence of the nodus-position in the fore- and hindwing already started within those “Zygoptera”, which possessed fore- and hindwings which are not yet differently broadened in the proximal region. Then, during further enhancements of the wing path steepness (and the wing stroke frequency) in Anisozygoptera and Anisoptera in both flight segments different means seem to have been used to ‘harmonize’ the relation of lift/forward thrust-production of the proximal/distal wing. One of these means is the broadening of the proximal wing in the case of the Anisoptera, which is more limited in the forewing on account of its spatial relation to the hindwing. Another one can be seen in the extreme positions of the nodus in the case of *E. superstes* – maybe as an alternative way, since here the wing bases have been broadened much less markedly.

The similarity between *E. fatime* and Anisozygoptera + Anisoptera in the different position of the nodus in the fore- and hindwings supports the hypothesis of a phylogenetic relationship which has been deduced from the comparison of the clasping apparatus. At least the Euphaeidae can now be substantiated as most closely related to Anisozygoptera + Anisoptera; therefore a group Heteronoda has been constituted (Fig. 19). Fraser’s hypothesis of paraphyly of the Zygoptera is supported by this in principle, but his system needs to be changed in details: it is now necessary to clear up the phylogenetic relationship of the further groups of the “Calopterygoidea”.

In Figure 19 the monophyletic group Anisozygoptera + Anisoptera has been designated ‘Neoconjuncta’. This name is dedicated to Syoziro Asahina, whose studies on *Epiophlebia* have been fundamental. Designations with the background of a monophyletic group Zygoptera – Lohmann (1996: 214) e.g. put emphasis on this point when creating the name “Epiprocta” – are not adopted here.

Interdependent evolution of constitutive characters

The new phylogenetic position of *E. fatime* was (partly) substantiated through the anatomical and functional characters of the male clasping apparatus and the special type of tandem linkage, which could well represent the starting point for a linkage-shifting evolution that has led to the anisozygopteroid-anisopteroid state. Several characters of the epallagoid system have been decisive. Some of these are represented indeed in other

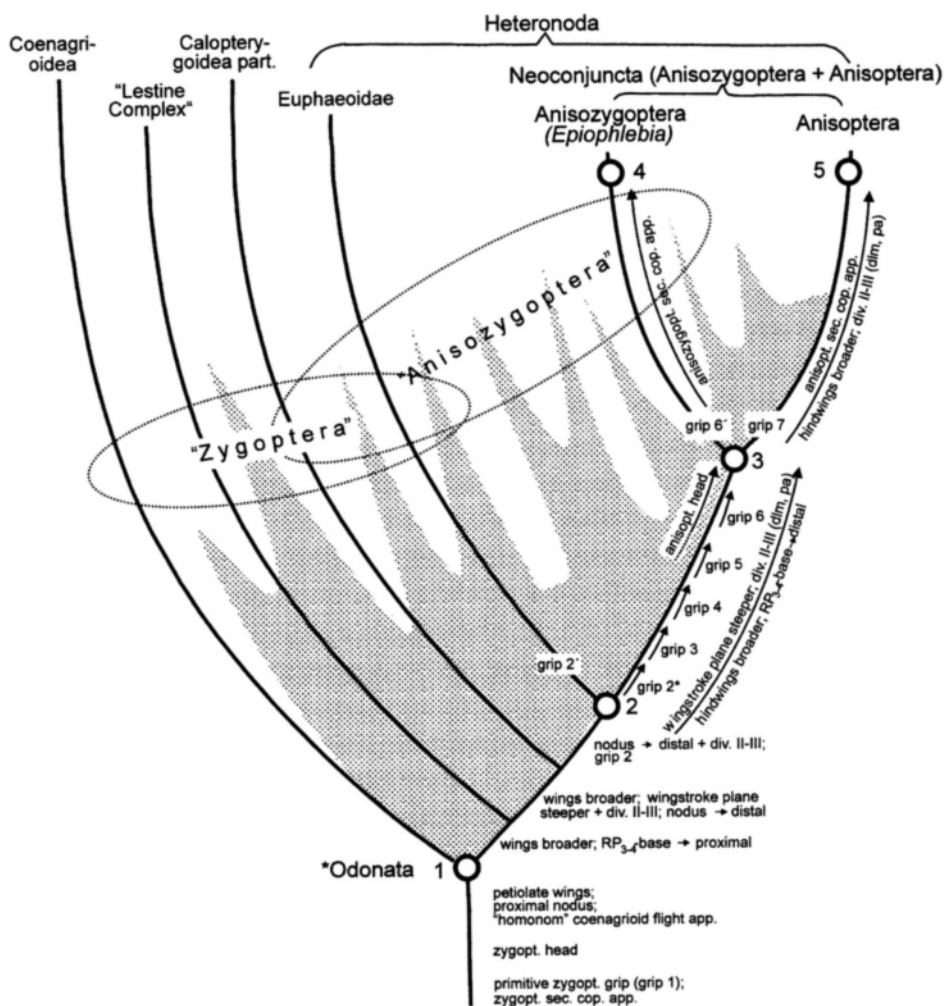


Figure 19. Phylogenetic tree of the Odonata — multiple paraphyly of the Zygoptera and evolution of different constitutive characters of the sub-groups. For 'homonom' coenagrioid flight apparatus and the different functions of the muscles dlm and pa in the meso- and metathorax, see Pfau 1986: 61f. — div: divergence; sec. cop. app.: secondary copulatory apparatus (cf. also Pfau 1971); II: mesothoracic segment; III: metathoracic segment; grip 2* – grip 5: cf. Figure 17; grip 1: to far extent lestoid-calopterygoid grip, the cerci and the paraprocts gripping the female pronotum; grip 2': epallagoid grip; grip 6': epiphlebioid grip; grip 7: to far extent aesthnoid grip; RP₃₊₄: radius posterior 3-4 (= Radius 4+5 in Fraser 1967; for evolution cf. Pfau 2000). 1-5: stem species of *Odonata (1), *Heteronoda (2), *Neoconjuncta (3), *Anisozygoptera (4) and *Anisoptera (5).

groups of Zygoptera: e.g. a narrow relationship of the lamina accessoria and the cercus can be found in the Lestidae (Fig. 11d), an oblique muscle mC2 occurs also in *P. nymphula* (Coenagrionidae) (Fig. 11c), *Platycnemis pennipes* (Pallas) (Platycnemididae) or *Elattonneura glauca* (Selys) (Protoneuridae), the reduction of the function of the paraprocts

can be supposed for e.g. *P. nymphula* and different *Lestes*-species and a clamping of the male cerci to serve for stabilization of the linkage can be expected for *P. pennipes*, *Coenagrion puella* and *Lestes*-species (Knitter 1998: figs 2, 3). However in these cases the characters mentioned above occur not in combination, whereas they are combined in *E. fatime*. Above all: they are combined in *E. fatime* with an alteration of the spatial relationship between the cercus-leverpoints and the lamina accessoria+epiproct.

Certain characters of the flight apparatus have been added here as synapomorphies of a monophyletic group 'Heteronoda' (Fig. 19) to the characters of the clasping apparatus of *E. fatime*. This indicates a correlated and interdependent evolution of the linkage- and the flight-type – which could be similar to the assumed interdependent evolution of the secondary copulatory apparatus and the flight, mentioned in the last chapter. One could expect that *E. fatime* needed a certain improvement of the stability of its tandem linkage in parallel to the improvement of its forward flight capabilities. Indeed *E. fatime* can execute particularly quick forward flights, probably on account of the above mentioned apomorphic features of its flight apparatus. In Turkey I could observe that males of *E. fatime* flew so fast (approximately up to 4 m/sec), that I could hardly differentiate them from tiny blue libellulids, *Trithemis festiva* (Rambur), which flew at the same rivulet.

The mode of action of the cercus in *E. fatime* is most note-worthy in this context, since the essential cercal gripping force is directed more parallel (i.e. less perpendicular) to the flight direction. Therefore the male is able to counterbalance moments of inertia that result either from the reluctance of the female and/or his own flight acceleration. There seems to exist a correlation between the acquisition of a stronger forward flight and this special male grip with its new direction of gripping force. A further feature is the possible clamping of the cerci by the mesonotum of the female, which should interest theorists of sexual selection.

It is reasonable that the newly evolved main force-direction of the cercus grip parallel to the line of flight, acquired in *E. fatime*, also was a most essential feature for the development of the capability of the epiproct to assist in linkage-stability, since a cercal opponent force against the epiproct (which works in the mediosagittal plane) would have been present from the beginning on. The enlargement of the epiproct-lever in the further evolution, and the epiproct-shifting to the female's head, seem to have had good chances to evolve, since the epallagoid cercal grip to the hind margin of the female pronotum in all steps of the evolution produced the essential opponent force to the epiproct.

In the stem group of the Anisozygoptera + Anisoptera the further evolution of the tandem linkage presumably was also 'driven' in parallel to the further evolution of the forward flight capabilities (Fig. 19). In turn the acquisition of the special tandem grip onto the head could have been a prerequisite for the further alterations of the flight system, since the advantages of the new linkage type are evident: gripping the head means to grip a most complex sensory system measuring gravity (Mittelstaedt 1950, Gorb 1998). For the female, which besides this is now dragged from her anterior end, it is now risky to resist the male guidance on account of her sensible and soft neck region. This means that the energy input of the male in the grip, mainly via mC1-contraction, in principle could be reduced as soon as the grip to the head has been evolved. Indeed, the former opposition 'cerci-against-epiproct' via the complicated epallagoid movement of the cerci was secondarily changed at the base of the Anisozygoptera + Anisoptera.

In the Anisoptera the emphasis of participation has finally been transferred from the cerci to the epiproct (\rightarrow mC1-shifting), whereas the movability of the cerci in the (new) joint $j_{c_2-t_2}$ has soon been limited by stops: the opposing role of the cerci to the epiproct has been made by this more or less 'automatic'.

There is an ironic tinge: evolution that started from a constellation of characters in which the females are able to assist in the tandem linkage-stability via clamping has finally led to a constellation in which the female's role is probably markedly diminished.

Discussion

In the Introduction different hypothetical possibilities have been mentioned. Concerning my former doubts that a small zygopteroid epiproct has been secondarily enlarged in the Anisozygoptera + Anisoptera, all results now point just in this direction: There is no indication that the epiproct could have started off as a large structure at the base of the *Odonata. Instead, starting as a small sclerotized knob, without any gripping function, the epiproct must have been transformed step by step into a gripping structure during the evolution which led to the Anisozygoptera + Anisoptera, finally even acquiring a predominant function; within that evolution the grip must have shifted from the female prothorax to the head.

This study therefore also touches the question to what extent a more precise knowledge of the functional morphology of structures and systems will be valuable in the future – not only for attaining a more complete picture of the functional interdependences of the body systems and their alterations during the evolution, but also for the substantiation of phylogenetic hypotheses.

The functional morphology has obviously been neglected in the field of phylogenetics. In the case of the Odonata the flight apparatus e.g. turns out more and more as having played a superior role during evolution. Therefore this system should be taken into consideration in evolutionary scenarios and phylogenetic evaluations. However, when looking into the literature one gets the impression that no forward step has been made in decades. Looking e.g. at the mistaken models of the wing stroke- and pronation-supination-movements (Weber 1933; also Pfau 1991: fig. 8) – which curiously continued to exist up to now in textbooks (e.g. Gewecke 1995) – it is obvious that some modern results, which had been published in the meantime, have constantly been ignored. The pronation- and supination-movements of the wing, e.g., were thought to result in the first line from an antagonistic activity of the direct wing muscles (basalar and subalar muscles) which should rotate the wing as a whole around its longitudinal axis, and, coordinated to this, also manage the stroke. Relying on this incorrect model means ignoring the capability of the odonate wing to function like a variable-pitch propeller (Pfau 1986, 2000; besides this the hypothesis of a direct stroke mechanism via the basalar- and subalar-muscles is erroneous). A wing which rotates as a whole around its longitudinal axis is not able to adjust adequately to the air current – however a wing which is twistable like a propeller and in which certain muscles are able to affect the distal wing area to a different degree than the proximal area, certainly is. This capability of adjusting the whole wings shape according to the air currents, which to a large degree is independent of the stroke, seems to have been of prime importance for the odonates to evolve a quick

forward thrust flight via an alteration of the thorax-defined angle of the wing stroke-plane; via the shifting of the nodal point (the nodus) of the 'propeller-wing' the bi-partition of the wing in a proximal part (mainly for lift generation) and a distal part (mainly for forward thrust generation) could be modified in parallel, balancing the altered lift-to-forward thrust-relation. This evolution resulted in divergences between the two thoracic flight segments and between the fore- and hindwings (→ 'Heteronoda'). These apomorphous acquisitions concerning the flight performance within the Odonata are now interpreted as having been interdependently linked to the evolution of other body systems. There are indications that they led to fundamental transformations of the clasping apparatus and male-to-female linkage within the stem group of the Anisozygoptera + Anisoptera ('Neoconjuncta').

Some authors today even deny a significance of functional morphology in the field of phylogenetics. However, the hope that the 'modern method', which is based on the processing of large quantities of supposedly apomorphous or plesiomorphous characters (which are picked up by random sampling – in many cases without a deeper understanding of function and functional correlation to one another) by computer, would lead to well-substantiated phylogenetic unities seems to be optimistic. In addition, in the case of Odonata a complicated evolution in detours presumably took place (Pfau 2000: fig. 5; shifting of nodus-position) which will resist clarifications by simply using a formalistic outgroup-comparison method. In the future the progress of functional morphology, of course combined with information from different other fields of science, should be incorporated to a larger extent. This will lead to more profound insights into the evolution – and it will improve the phylogenetic systems as well.

Conclusions

Arguments are given that the primitive clasping apparatus and tandem linkage of the *Odonata (i.e. of the stem species of all extant Odonata) in principle was lepto- or calopterygoid. Hence it follows that the evolution of the anisozygopteroid-anisopteroid type of clasping apparatus and linkage began with an epiproct which was small and situated dorsally of the cercal lever-points. The evolution of the systems of *Epiophlebia superstes* and Anisoptera therefore required as a first step an epiproctal movement reversal (EMR), for which the clasping apparatus and linkage of *Epallage fatime* (Euphaeidae) can be seen as an initial stage.

E. fatime shows some very peculiar features in its clasping apparatus and tandem linkage, which are considered as preadaptive for the start of the evolution towards the anisozygopteroid-anisopteroid systems: The opener muscle of the cercus is strongly oblique; correlated to this the lever-points of the cerci are translocated dorsally in relation to the lamina accessoria + epiproct. There is a joint between the lamina accessoria and epiproct (j e-la). The paraprocts show shortened paraproctal prongs, which have lost their gripping function. Only the cerci grip the female in a highly specialized way, the large cercal hooks extending behind the female pronotum medially. The grip-force of the cercal hooks is exerted mainly ventrad (with respect to the male), i.e. in parallel to the mediosagittal plane. Only in this way the cerci could be usable to become opponent

structures of a newly evolved epiproctal grip – which operates in the mediosagittal plane – in the stem group of the Anisozygoptera + Anisoptera.

It is expected that during certain quick flight actions of the pairs of *E. fatime*, e.g. during the ‘water-dipping flight’, the female is able to fortify the linkage by clamping the male cerci while closing the pro-mesothoracic cleft by contraction of the dorsolongitudinal muscles between pro- and mesothorax.

In the stem group of the Anisozygoptera + Anisoptera (Neoconjuncta) the EMR led to a co-ordination of the closing movements of the cerci (muscle mC1) and the lamina accessoria + epiproct (muscle mLa1). Furthermore the new clasping function of the epiproct proceeded via a reduction of its ventral membraneous movement-clearance in the region of the lamina supraanalis. A new opener muscle of the epiproct could evolve by specializing the former lifting-muscle of the lamina supraanalis (mLa2). This muscle now opens the angle between the lamina accessoria and the epiproct by moving the joint j e-la between the dorsal and ventral suspensions of the system caudally. Since this also opens the cercus, the former cercal opener muscle could be reduced; it is still present as a vestige in juvenile *E. superstes* showing its former epallagoid obliqueness. Following the EMR the epiproct was elongated in the stem group of the Anisozygoptera + Anisoptera step by step; its grip was shifted along the female pronotum towards the head. The epiproct attained a grip on the female head and the cerci lost their grip on the hind margin of the female pronotum – however not before a lateral cercal process had also reached the head, preventing its caudal rotation.

The function of the paraproctal prongs presumably has been reduced early during this evolution (cf. *E. fatime*); nevertheless a paraproctal prong could have persisted even after the linkage shifting for a long time. The paraproctal prong is absent in the extant Anisozygoptera and Anisoptera; a vestige is detectable e.g. in the males of *Aeshna cyanea*. Instead a membraneous medial lobe on the paraproct is evaluated as newly formed on account of its presence in males and females of *E. superstes* and Anisoptera.

E. superstes is evaluated as a transition stage: the main closer muscle mC1 of its clasping apparatus is in a zygoteroid state, already inserted on the cercus; the epiproct is proximally broad showing a lateral joint to the cercus, which supports the connecting joint between the lamina accessoria and the cercus; the paraproctal base is still integrated in the kinematic system.

In the stem group of the Anisoptera the insertion of the main closer muscle mC1 has been translocated to the epiproct. Now this muscle moves mainly the epiproct, and – in more advanced groups – only the epiproct. The epiproct could get proximally smaller, loosing its former joint-connections to the cerci. The cercus developed a new joint to the tergum. The paraprocts (to far extent) are not integrated any more as suspension-elements of the cerci in the function of the clasping apparatus.

An interdependent evolution of the flight apparatus and the clasping apparatus + tandem linkage is assumed, which led to new characters in both systems. In *E. fatime* the steep basic wing stroke-plane which is differently steep in the meso- and metathorax – correlated to a distal position of the nodus which is different in the fore- and hindwings – indicate apomorphic capabilities to perform a quicker forward flight (cf. also Pfau 2000). On the other hand the clasping apparatus of *E. fatime* secondarily attained a strong force component of the cerci, which is directed largely in the direction of the flight of the

pair; in antecedent zygopterans it is directed essentially transversely to it. This improved the capability to pull the female which can be interpreted as an adaptation to the newly acquired capabilities for a quicker forward flight.

On account of the synapomorphous characters of (at least) the Euphaeidae and the Anisozygoptera + Anisoptera the Zygoptera are evaluated as a paraphyletic group, in principle conforming Fraser's hypothesis (Fraser 1954, 1957), however different with respect to the arrangement of the groups.

Acknowledgements

I am much indebted to my wife Beate and to Michael May and Wolfgang Schneider, who spent a lot of time to improve the English of my text.

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